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Foreword by C. W. STILES, Professor of Zoology, United States Public Health Service.

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HYDROGEN-ION CONCENTRATION AND THE DISTRIBUTION OF *LIMNAEA TRUNCATULA* AND *L. PEREGRA*, WITH A NOTE BEARING ON MOSQUITOES.

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AND

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DURING the past few months we have collected a considerable amount of information relating to the value of *p*H as affecting the distribution of the three species of *Limnaea* commonly found in North Wales. Tables I and II show that *L. truncatula* occurs over a range of *p*H 6·0 to 8·6, and *L. peregra* 5·8 to 8·8; *L. palustris* was recorded from 7·4 to 8·0 (but only three of the readings included this species).

Atkins and Lebour (1924) record observations on sixteen water samples drawn from very widely separated sources, stating that "the data presented ....are obviously not so numerous as could be desired." Our observations extend and amplify these records, since they only found *L. truncatula* in water of *p*H range from 6·4 to 7·8 (a reading of 5·8 is given as that of the soil on which the molluscs were found) and *L. peregra* from 6·6 to 7·7.

It is our opinion that in view of the more extended range of hydrogen-ion concentration of both these species now recorded, together with the evidence available in relation to mosquito larvae, that hydrogen-ion concentration is not of vital importance for these forms of animal life. The fact remains that differential distribution does occur, since *L. truncatula* and *L. peregra* are seldom found together, although they may be abundant in contiguous environments, and some overlapping may occur at times. One of us, after a very considerable experience of *Limnaea* in Mid- and North Wales, and elsewhere, has already expressed the view that "In *L. truncatula* the foot is small and the shell a narrow spire, while in *L. peregra* the foot is relatively much broader as also is the shell. *L. peregra* is able to travel over the surface of soft mud in which *truncatula* would sink, as is readily observable during the progress of field and laboratory work....*L. truncatula* will leave a soft substratum for a harder if food be there available, as for instance fallen leaves that have become coated with a deposit of diatoms; it dislikes the soft mud on which *peregra* dwells, and will crawl from it, if possible." (Walton, 1917.)

Observations made during the course of the present investigations confirm the opinions cited in the preceding paragraph. For example, we have never found snails in peat cuttings, even if long abandoned; while the *p*H of such cuttings has a range from 5·6 to 7·5, the bottom is always similar, being extremely soft and flocculent.

The major portion of the readings here recorded were taken in the field, the remainder were made in the laboratory within not more than twelve hours of collection of the sample: most well within that time.

The method used was a colorimetric one, the apparatus being the "Capillator" manufactured by British Drug Houses, Limited. Preliminary tests were made with the "B. D. H. Four-Eleven Indicator" to determine which of the indicators to use for the more accurate determination; for this second determination one of the following indicators was used: bromo-cresol purple (*p*H 5·2 to 6·8), phenol red (*p*H 6·8 to 8·4) and thymol blue (*p*H 8·0 to 8·6). The equipment at our disposal did not permit of determinations of conductivity, etc.

The total range of *p*H observed was from 5·6 to 8·8. The maximum number of readings are 7·4–7·6, and these maxima correspond with the maxima for *L. truncatula* and *L. peregra*, as is graphically indicated in Table II.

Note on Table II. The method adopted for the determination of *p*H only enabled direct determinations to be made at alternate decimal places; readings to a single unit of decimals were made by interpolation. In the construction of Table II, it was decided to economise space by recording only *even* decimals, and the *odd* decimals, which are given in Table I were "rounded off" by alternately adding or subtracting a unit. For example, in the field, *p*H 7·5 was taken as the value for a colour reading apparently mid-way between 7·4 and 7·6 of the standard tubes; in compiling Table II, alternate readings of 7·5 were entered as 7·4 and 7·6.

NOTE BEARING ON MOSQUITOES.

We have previously referred to the subject of hydrogen-ion concentration and mosquito larvae. MacGregor (1921) has reported experiments which led him to believe that tree-hole breeders required an acid range of *p*H while surface-water breeders required an alkaline range. These experiments have been repeated, but the original observations have not been confirmed. Thus, one of us placed larvae of *Aëdes detritus* in water adjusted, by addition of acetic acid, to a *p*H of about 4·2. The larvae remained alive in this water for a considerable period, until it dried up.

In other experiments, larvae of *Culex pipiens* were placed in water at *p*H 4, 7·5, and 9 + , and larvae of *Anopheles maculipennis* at 4 + , 7·5 and 10 + , with very similar results.

Field results apparently indicate that mosquitoes in various parts of the world can tolerate a considerable range of *p*H; thus Senior-White (1926) records *Anopheles maculatus* as having a *p*H range of 9·8 + to 9·4 + and *Stegomyia albopicta* (a species breeding in broken coconut shells) a range of from 4·6 − to 9·44. Barber and Komp (1922) have shown. also. that the

ERRATUM.

Parasitology, Vol. XVIII. p. 364.

Third line from bottom: "*p*H range of 9·8 + to 9·4 + "
should read "*p*H range of 5·8 + to 9·4 + "

three common Anopheline mosquitoes of Alabama can breed in waters having a *p*H range of from 5·0 to 8·0 which was the range of the natural waters examined.

Since the above was written a paper by Morishita (*Rev. Appl. Ent. B.* XIV. pp. 114, 115, July 1926) has been reviewed. This writer concludes from a study of *Culex fatigans* that "the hydrogen-ion concentration of the environment is of little importance as a factor in the development of this species."

Table I.

(In the column headed "Snails," species are denoted by the letters t.—*L. truncatula*, p.—*L. peregra*, l.—*L. palustris*.)

No.	Date	Locality	Altitude	*p*H	Snails	Remarks
1	28. x. 25	Tremadoc	700	6·0	t.	Wet place in field
2	4. xi. 25	Llangoed	400	7·5	t.	After very heavy rain
3	20. i. 26	Holland Arms	20	8·5	t.	Small pool, margin of stream, history of Liver Rot
4	,,	Bangor	50	8·8	p.	Slate tank with weed
5	26. i. 26	Holland Arms	50	8·0	t.	Pools, edge of ditch. Heavy soil. History of Liver Rot
6	,,	,,	35	8·0	l.	Flood-water that dries up in summer. History of Liver Rot
7	,,	,,	35	7·5	—	Ditch. Decaying vegetation
8	3. ii. 26	Bodorgan	150	7·3	t.	
9	4. ii. 26	Glasfryn	900	7·3	t.	Shallow stream on drift clay
10	,,	Pentre Voelas	800	7·5	p.	Roadside ditch
11	,,	Yspytty Ifan	750	7·5	—	Peaty soil over drift clay
12	,,	Pentre Voelas	700	7·6	t.	Roadside ditch, much grass, dries in summer
13	11. ii. 26	Llanfaglan	40	7·5	t.	Farm ditch. History of Liver Rot
14	10. iii. 26	Llanllechid	700	7·3	t.	Swampy unimproved pasture. Peat over drift clay. History of Liver Rot
15	,,	,,	650	6·9	p.	Stagnant ditch, soft flocculent bottom
16	,,	,,	600	7·4	t.p.	Slow swampy ditch, flocculent bottom. History of Liver Rot
17	,,	,,	600	7·2	—	Pools near last. Peat over drift clay
18	,,	,,	550	7·4	t.p.	Farm leet. Snails abundant on muddy edge
19	,,	,,	500	7·2	t.	Peaty pool by ditch. History of Liver Rot
20	,,	,,	450	7·0	—	Semi-stagnant alder swamp
21	,,	Halfway Bridge	200	7·5	—	Small field stream near River Ogwen
22	,,	,,	150	7·0	—	River Ogwen, full, but not in flood
23	17. iii. 26	Vaynol Park	150	7·7	t.p.	Ditch in wood, clay soil. Liver Rot
24	,,	,,	150	7·8	t.	Fields near 23. History of Liver Rot
25	23. iii. 26	Pontllyfni	25	7·0	—	Peaty drain leading to stream. Near sea
26	23. iii. 26	,,	25	7·3	—	Small stream near 25
27	,,	,,	40	6·3	—	Peaty hollows by stream. History of Liver Rot
28	,,	,,	40	7·4	p.	Stream by 27
29	,,	,,	75	7·7	p.	Spring, farm water supply
30	,,	,,	75	7·5	t.	Wet hollows near 29. History of Liver Rot
31	,,	,,	150	7·5	p.	Muddy pool in lane

Table I (*continued*).

No.	Date	Locality	Altitude	*p*H	Snails	Remarks
32	2. iv. 26	Dolgelly	20	7·5	t.p.	"Borrow ditch" railway embankment
33	,,	,,	20	7·5	—	Field pool
34	,,	,,	20	7·6	p.	Pool near above
35	6. v. 26	Llanfaglan	25	8·2	—	Ditch, *Lemna*, watercress, etc. History of Liver Rot
36	,,	,,	50	7·4	—	Pool by stables. Mosquitoes every summer
37	6. v. 26	,,	25	8·1	p.t.	Pool fed by stream. *Paludestrina jenkinsii*
38	,,	,,	20	7·0	—	Swampy patch near sea. t. formerly before treatment
39	,,	,,	18	6·8	—	Saltmarsh ditch. *Aëdes detritus*, reddish flocculent bottom
40	7. v. 26	Lake Ogwen	984	7·7	—	Near stream infall, after heavy rain
41	,,	Glasfryn	900	7·4	t.	(Same place as No. 9)
42	,,	,,	1000	7·4	—	Sheep walk, surface water
43	,,	,,	850	5·6	—	Old peat diggings. Cotton grass
44	,,	Pentrefoelas	800	7·6	t.	(As No. 13)
45	11. v. 26	Bangor	50	7·8	l.	Stream. Soft bottom
46	,,	,,	50	7·3	t.l.	Marsh. *Planorbis* sp.
47	17. v. 26	Near Chwilog	400	5·8	—	Peat bog. *Caltha*
48	,,	,,	410	6·8	—	Margin of lake. Sphagnum, etc.
49	,,	Afonwen	50	7·5	p.	p. very large. t. formerly. History of Liver Rot
50	17. v. 26	Brynkir	280	7·4	—	Peat bog
51	29. v. 26	Bangor	250	7·8	p.	Roadside ditch
52	2. vi. 26	Malldraeth Marsh	15	7·6	p.	Muddy ditch. *Physa*
53	,,	,,	16	7·5	—	Wide slow ditch near river. *Planorbis*
54	3. vi. 26	Pantglas	440	7·2	p.	Ditch. Soft mud. *Equisetum*, *Poa fluitans*
55	,,	,,	420	7·7	—	Water of Afon Dwyfach
56	,,	,,	500	7·8	p.	Roadside ditch. Algae. Snails small
57	,,	,,	500	6·1	p.t.	Ditch, semi-peaty hollows. *Juncus*, Cotton grass, etc. Snails very small
58	,,	,,	500	6·0	t.	Near last. Peaty hollows. Snails small
59	,,	,,	450	6·0	—	Marshy bottom, same field. "Amber" water. *Menyanthes*, *Comarum*, *Pedicularis palustris*
60	,,	,,	500	6·8	p.t.	Muddy pools, wet meadow. t. few, p. abundant. *Juncus*
61	,,	,,	550	7·5	t.	Semi-peaty pools near last. *Juncus*, Cotton-grass, etc. History of Liver Rot
62	,,	,,	430	7·5	p.	Peaty ditch, hard bottom. *Equisetum*, etc. p. large
63	,,	,,	430	5·8	—	New peat cutting, flocculent debris, tinted water
64	,,	,,	430	6·8	—	Old peat-cutting near last. Soft bottom
65	,,	,,	500	7·1	—	Peaty ditch, deep soft bottom
66	23. vi. 26	Llanllechid	600	7·2	—	(No. 16)
67	,,	,,	680	7·9	—	(No. 15)
68	,,	,,	700	7·9	—	(No. 14)
69	,,	,,	500	7·9	p.t.	(No. 18)

Table II. (*Explanation in text.*)

*p*H	No. of readings	Occurrence of snails		
		L. truncatula	*L. peregra*	*L. palustris*
5·6	/			
5·8	//			
6·0	////	///	/	
6·2	/			
6·4				
6·6				
6·8	////	/	/	
7·0	/////			
7·2	///////	//	/	
7·4	//////////////////	//////////	////	/
7·6	//////////////	/////	///////	
7·8	///////	/	///	/
8·0	////	//	/	/
8·2	/	/	/	
8·4				
8·6	/	/	/	
8·8	/		/	
Totals ...	69	26	21	3

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(*MS. received for publication* 1. VII. 1926.—Ed.)

A NOTE ON THE GENERIC NAME OF THE SPIROCHAETE OF SYPHILIS (*TREPONEMA PALLIDUM* SCHAUDINN, 1905).

By CLIFFORD DOBELL, F.R.S.

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In a note which I contributed in 1918 to *Special Report, No.* 19 of the Medical Research Council, I attempted to show that the "correct" generic name of the spirochaete of syphilis—according to the Rules of Nomenclature—is *Spironema* Vuillemin, 1905. The premisses from which this conclusion was drawn were briefly set out in the publication cited, and need not be repeated here: but my argument—put very shortly—was that, since the Spirochaetes are Bacteria, and not Protozoa, their nomenclature must be determined by the Botanical Rules, not those of Zoology; and that of the three generic names proposed for the spirochaete of syphilis in 1905, *Spironema* has priority, and must therefore be accepted. (*Spironema* was proposed by Vuillemin in June, *Treponema* by Schaudinn in October, and *Microspironema* by Stiles and Pfender in December, 1905.)

A similar argument had been used earlier by Gross (1911); and in 1918 it appeared to me both valid and conclusive, provided that the name *Spironema* had not previously been bestowed upon any plant. On this point Gross, after looking into the matter, had made the following statement: "Im botanischen System.....war der Name *Spironema* noch nicht okkupiert, als Vuillemin ihn....in Vorschlag brachte" (Gross, 1911, p. 113). As I knew Gross personally to be an accurate and trustworthy worker, I accepted his words and did not, unfortunately, myself make an exhaustive inquiry into the genus *Spironema* from the botanical standpoint. I searched the literature on the Schizophyta, Algae, and Fungi, however, and could find no record of a *Spironema* among these organisms. Accordingly I wrote (*loc. cit.* p. 48) "As no plant appears to have been named *Spironema* prior to 1905, Vuillemin's name is therefore valid, and must stand."

It has now been pointed out to me, however, by Dr C. W. Stiles of Washington, that the generic name *Spironema* had already been introduced into botanical nomenclature—for flowering plants—on at least three occasions prior to 1905. Dr Stiles states (*in literis*) that the name "was published, first, by Rafinesque in 1836 for a genus of the family Lauraceae; second, by Lindley in 1840 for a genus of the family Commelinaceae. In addition the unpublished name *Spironema* of Hochstetter was cited in 1842 by Hochstetter as a synonym

of his *Cyclonema*, a genus of the family Verbenaceae." At my request Dr Stiles kindly supplied me with more exact references, which he had personally verified at Washington: and with considerable difficulty I have now been able to re-verify these references myself. (I append his citations, which I have carefully checked, for the information of others.)

It is therefore clear that the name *Spironema* was preoccupied in botany, as it now notoriously was in zoology, when Vuillemin proposed it in 1905. Both Gross and myself were in evident error when we accepted it as valid for the spirochaete of syphilis. I do not know what the precise status of the name *Spironema* is in botany to-day. (Willis (1925), I note, accepts the Lindleyan genus.) But in any case I can now only endorse the opinion of Dr Stiles when he writes that "the name *Spironema* is absolutely dead" for the spirochaete of syphilis, "no matter whether one views it as an animal or a plant."

Since the name *Spironema* is not available, it follows that the correct generic designation of the organism in question is *Treponema* Schaudinn, 1905 —since this name has priority over *Microspironema* Stiles et Pfender, 1905.

To Dr C. W. Stiles I offer my sincere thanks for pointing out my error to me in private, and so enabling me to rectify it in public. I now agree with him that the proper generic name of the spirochaete of syphilis is not *Spironema* but *Treponema*, and that this organism should henceforth be called *Treponema pallidum* Schaudinn, 1905—unless some future delver into the literature should unearth some other valid but as yet unknown substitute, and provided that the reactionary proposal of certain recent French and German writers to revert to the name *Spirochaeta* be not generally accepted.

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THE PROBLEM OF THE ORIGIN OF NEMATODES.

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Introduction.

The systematic position of Nematodes is an old standing problem which has already received much attention from zoologists. The conclusions at which they have arrived are however very discordant and the most widely separated orders of Metazoa have been claimed as near relatives of Nematodes. This great divergence of opinion has not abated the general interest in the problem, but, on the contrary, has had a greatly stimulating effect as was shown recently at the British Association for the Advancement of Science (1923) in a discussion on the affinities of Nematodes, opened by Prof. Hickson and supported by Prof. Goodrich and Dr Baylis. The results of this discussion were soon afterwards incorporated by Dr Baylis in a very interesting paper containing a complete review of the problem as well as a statement of the author's own views.

In the present paper I propose to discuss two subjects: (*a*) the relationship between the free-living and parasitic Nematodes, this being more intimately connected with the main problem of the affinities of the whole group than it would seem to be at first sight, and (*b*) the more recently assumed relationship between the Nematodes and Arthropods.

Before discussing these subjects we may examine briefly a few striking Nematode characters. The Nematodes form a group of Metazoa widely differing in structure from all other Invertebrates and showing an extremely varied mode of life. Nematodes comprise two main ethological groups: (*a*) free-living, and (*b*) parasitic forms. The free-living Nematodes inhabit all kinds of waters, soils, and decomposed organic substances. The parasitic forms live in plants and in representatives of all orders of the animal kingdom (Invertebrates and Vertebrates). Further, they show every possible transition between the free-living and parasitic mode of life. Nematodes may be: (1) free-living throughout their life-cycle, (2) parasitic throughout their life-cycle, (3) parasitic in the adult stage and free-living in the larval stage, (4) parasitic in the larval stage and free-living in the adult stage, (5) parasitic and free-living in alternating generations, and (6) parasitic on their own species where the male lives as parasite within the female. Again, the parasitic forms exhibit great variety in their life-cycle ranging from a simple cycle in

one host within whose body no migration occurs, to a life-cycle complicated by a period of migration within the body of the host and a period of development in an intermediate host. Parasitic Nematodes often reach a high degree of equilibrium in relation to their host, as shown by the host's great tolerance to a massive infection by these parasites. They often exhibit a series of important physiological adaptations, such as (1) protection against the proteolytic enzymes of their host, (2) anoxybiotic mode of life, and (3) great vitality and longevity in their larval stages.

THE RELATIONSHIP BETWEEN THE FREE-LIVING AND PARASITIC NEMATODES IN THE LIGHT OF DOLLO'S LAW OF IRREVERSIBILITY OF EVOLUTION.

The problem now arises as to how the Nematodes, notwithstanding the great diversity in their mode of life, have developed such a striking uniformity in their morphological and cytological characters. How is the morphological similarity of free-living and parasitic forms to be explained? We know that whenever parasitic and free-living forms occur in other groups of animals, that the former show a series of clear morphological characters denoting parasitic specialisation. This is the case in Protozoa (Flagellates, especially Dinoflagellates, Ciliates), Crustacea (Copepoda, Cirrhipeda and Isopoda), Insecta (Diptera and Hymenoptera), and Mollusca (Gasteropoda).

The absence in Nematodes of distinct morphological characters connected with their parasitic mode of life can be understood, however, if we assume that the free-living Nematodes are not primitive but are derived from parasitic forms by a secondary readaptation to the free mode of life. According to this supposition the Nematodes would be derived from a group of free-living organisms which have gradually adapted themselves to parasitism. In consequence of parasitic adaptation the whole structure of these animals has undergone a very marked modification which may be termed "parasitic specialisation." Subsequently, for an unknown reason, some of these parasitic forms have gradually reverted to the free mode of life, in other words have become free-living by a secondary readaptation. They have not, however, reacquired the characters of the primitive free-living group to which they at first belonged, but have readapted themselves to the old mode of life with the means afforded by their specialised new morphology.

The history of Nematodes seems therefore to follow Dollo's generalisation that the evolution is irreversible. According to this generalisation (which is amply supported by anatomical and palaeontological studies on numerous Vertebrates and Invertebrates) an organism, which has changed its mode of life and undergone morphological modification, on returning to its old mode of life does not reacquire its old characters but readapts itself to the old conditions of life by new means.

The argument for a parasitic origin of the free-living Nematodes is supported also by the following considerations:

(1) The free-living forms are not always provided with spines or cuticular

projections. Many of them are completely devoid of external ornamentation and in this respect do not differ from parasitic forms.

(2) Free-living Nematodes display a very great variety in their mode of locomotion (Stauffer, 1924). The cuticular projections and various organs of fixation, when present, are of heterogeneous origin and cannot be homologised with the primitive appendages. Moreover, the great diversity in the ambulatory adaptations of this group denotes that here the locomotion is the result of a secondary adaptation to the active mode of life; it indicates that these animals have passed through a mode of life, such as parasitism, during which they have lost their primitive appendages and that they were obliged to readapt themselves by various new means to the free mode of life (cf. Keilin, 1915).

(3) As to the relative numbers of the free-living and parasitic forms, Baylis states: "a survey of the literature shows that over 400 genera or sub-genera of free-living nematodes have been described (including a certain number wholly or partly parasitic in invertebrates), while the number of known genera parasitic in vertebrates probably scarcely reaches 300." Baylis uses this consideration in support of the view that it is "most probable that parasitic forms have been derived from free-living ancestors, and not the reverse." It seems to me, however, that these numerical data scarcely apply in the discussion of our problem, because the relative number of species or genera belonging to different ethological groups afford no indication as to their evolution. Moreover, these numerical data are far from being complete. For instance, the forms which are partly or wholly parasitic in Invertebrates ought to be included with the parasitic and not the free-living forms. In fact, the parasites of Invertebrates, especially of Insects, such as *Sphaerularia*, *Allantonema*, *Aproctonema* or *Bradynema*, etc. are the most highly adapted forms to the parasitic mode of life and perhaps the most highly specialised parasitic Nematodes. It is almost certain, on the other hand, that if the number of such parasitic forms hitherto described is limited, this is only due to the fact, that not being of economic importance the Nematode parasites of Invertebrates have seldom attracted the attention of helminthologists. We have sufficient indication, however, that a great number of such forms are still awaiting investigation.

The supposition of the relationship between Nematodes and Arthropods.

Among the Invertebrates, Arthropods, and especially Insects have been lately suggested as being ancestors of Nematodes. The view that Nematodes are derived from Arthropods has already been advocated by Bütchli, E. Perrier and Maupas, and has latterly been supported by such authorities among helminthologists as Rauther (1909), Seurat (1920), and Baylis (1924). This view is mainly based upon the following characters in which Arthropods and Nematodes are stated to resemble each other: (1) presence of cuticular layer, (2) moults, (3) absence of real coelome, and (4) absence of cilia.

The value of these characters may now be considered:

(1) The cuticular layer in Nematodes is composed of a glucoprotein substance (cornein), soluble in alkali. It differs markedly from the chitin of Arthropods which is insoluble in alkali, and which is a polysaccharide composed of glucosamine units. A cuticular layer, similar to that of Nematodes, exists in some other Invertebrates, such as Rotifers, which, according to de Beauchamp (1909, pp. 89–97), have three kinds of cuticle differing in their solubility and resistance to alkalies and acids.

(2) The phenomenon of moulting in Nematodes and Arthropods is a direct consequence of the existence of the cuticular layer. It is of interest to observe, however, that in Insects the moult is not always correlated with the growth of the organism, but is often connected with polymorphism during development, with metamorphosis or even with abnormal metabolism during starvation (*e.g. Tenebrio* larvae). The presence or absence of moults can be hardly used, therefore, as a character indicating phylogenetic relationship between the groups.

(3) The absence of a real coelomic cavity is a character common to Nematodes, Acanthocephala, Rotifers, Platyhelminths and Arthropods; in other words, groups of Invertebrates which show no other interrelationship. This character, therefore, cannot be taken as indicating a relationship between Nematodes and Arthropods.

(4) The complete absence of vibrating cilia is a character common only to Arthropods and Nematodes. In Nematodes, according to Hetherington (1923, pp. 39–41), one can follow a very gradual atrophy of various portions of the system which in other Invertebrates form the vibrating cilia. The reduction and loss of motility of cilia in both groups is also partly correlated with the characters mentioned above, namely: the development of the cuticular layer and disappearance of a real coelomic cavity. Since the presence of vibrating cilia in the remaining groups of Invertebrates cannot be considered as a character giving any indication of their phylogenetic relationship, the absence of the cilia in Nematodes and Arthropods can only be considered as a purely convergent character.

None, therefore, of the four characters, just considered, supports the view that Arthropods and Nematodes are closely related. This conclusion is, moreover, supported by the existence of important distinctive characters, of which the following is an incomplete but sufficient summary: (1) the difference in the structure of the cuticle (this has already been considered); (2) the metameric structure, distinct in Arthropods, is absent in Nematodes; (3) the special structure of hypoderm and muscles in Nematodes is never found in Arthropods; (4) the nervous system is of two entirely different types; (5) the circulatory system, present in Arthropods, is absent in Nematodes; and (6) the excretory system is also of two distinct types.

As to the supposed close relationship between Nematodes and paedogenetic Dipterous larvae, advanced by some authors, it hardly deserves

serious discussion. In fact, Dipterous larvae like other Insects differ from Nematodes not only in the characters previously mentioned and common to all Arthropods, but in many other characters confined to Insects or Tracheates in general, such as the presence of tracheae, of Malpighian tubes, of the fat body, nephrocytes, oenocytes, etc. Moreover, the few paedogenetic Dipterous larvae known are invariably parthenogenetic, while in Nematodes the sexes are separate.

Though it appears to me that we cannot accept the view of the Arthropod origin of Nematodes, I do not propose to advance any other phylogenetic hypothesis which will be more acceptable.

All we can say at present is that the systematic position of Nematodes still offers a problem for further investigation. The assumption that the actually free-living Nematodes are derived from parasitic forms, and that the primitive free-living stock of organisms from which the latter have originated has completely disappeared, merely emphasises the difficulty in connecting the Nematodes with any known group of Invertebrates.

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THREE NEW CASES OF MYIASIS IN MAN IN THE NORTH OF ENGLAND.

WITH A SURVEY OF EARLIER OBSERVATIONS BY OTHER AUTHORS.

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Introduction.

The term "Myiasis" is generally used to indicate the presence of Dipterous larvae in the living body of man or other animals. "The form of Myiasis most commonly met with in the United Kingdom," writes Austen (1912), "is that of the alimentary canal, as the result of which living larvae or pupae, greatly to the distress and alarm of the patient, are discharged from the bowel. Cases of Myiasis of the nasal passages and frontal sinuses, the external auditory meatus, the subcutaneous tissue, and the urinary passages are apparently of quite exceptional occurrence in the British Islands." The following pages deal with three hitherto unrecorded cases, two of urethral and one of intestinal Myiasis.

Previous Records of supposed cases of Urinary Myiasis in England.

The earliest reference to a possible case of urinary myiasis in this country is that recorded by Turner (1725). On November 24, 1725, a poor woman came to crave Dr Turner's advice for a child about 16 months old, bringing with her a "worm," which she said the apothecary had just drawn out of the child's penis. The child, for several days before had suffered great uneasiness, which the mother called convulsions of the bowels. "The child was continually drawing up the lower limbs, and straining at both sphincters; the urine seemed to pass with difficulty for some days, till at last there came a total suppression, and the worm advancing, showed itself at the extremity of the urethra, when the apothecary was called up to help them. The insect measured above four

inches, resembling the 'worms' usually voided by the anus, of the 'earthworm' kind but whiter. The apothecary said that when he came to the child, he saw a prenatural body, which at first he knew not what to make of, hanging ½ inch out of the glans, and lying double in the passage: perceiving it farther advancing, he took hold of it, and with little difficulty drew it forth." And again—"The summer before the last, a woman showed Dr Turner an insect of the maggot species, with a crusty red galea over the snout, and a crescent or forked tail, which she had just then voided by the urinary passage."

A further doubtful case is referred to by Kirby and Spence (1828, p. 139): "A medical friend of mine, at Ipswich"—writes one of the authors—"gave me this winter an apode larva voided by a person of that place with his urine, which I now preserve in spirits and can show you when you visit me. It appears to me to belong to the Diptera order, yet not to the fly tribes (*Tanystoma* Latr.), but rather to the Tipulariae of that author, with which however it does not seem to agree so entirely as to take away all doubt. It is a very singular larva, and I can find none in any author that I have had an opportunity of consulting which at all resembles it....When given to me, it was alive and extremely active, writhing itself into various contortions with great agility. It moved, like other dipterous larvae, by means of its mandibles. Upon wetting my fingers more than once to take it up when it had fallen from a table upon which it was placed, the saline taste with which it was imbued was so powerful that it was some time before it was dissipated from my mouth."

The author's description of this larva runs as follows—"*Body*, three fourths of an inch in length, and about a line in breadth; opaque, of a pale yellow colour; cylindrical, tapering somewhat at each extremity; consisting of twenty articulations without the head: *Head* reddish brown, heart-shaped, much smaller than the following joint; armed with two unguiform mandibles; with a biarticulate palpus attached exteriorly to the base of each. These mandibles appear to be moved by a narrow black central tendon under the dorsal skin terminating a little beyond the base of the first segment; besides this, there are four others, two on each side of it, the outer ones diverging and much slenderer, and very short. The last or anal joint of the body very minute; exserting two short, filiform horns, or rather respiratory organs. I could discover, in this animal, no respiratory plates, such as are found in the larvae of *Muscidae*, etc. nor were the tracheae visible."

It is almost impossible to identify the larva from this brief description. Nevertheless it is interesting to note that the larva of *Thereva* also has a small though distinct head, followed by 20 segment-like divisions. The labrum is hook-like, and the mandibles also exhibit a hooked form. At the anal extremity are two small styliform processes. The *Thereva* larva, however, has a pair of prominent ventro-lateral bristles on each thoracic segment, and three pairs of bristles on the tenth abdominal segment. Similar bristles do not appear to have been present in the larva described by Kirby and Spence. The larva described in Kirby and Spence, as previously stated, was very active when alive; its movements may have resembled those of *Scenopinus* in being "serpent-like." The larva of *Scenopinus*, we are told, "resembles that of *Thereva*. It is amphineustic, white and vermiform. The head is brown and well-

developed, and is followed by 20 apparent segments. Most of the abdominal somites are sub-divided by a strongly marked constriction, thus giving the appearance of an increased number of segments; the terminal segment bears two small styles."

Possibly Kirby and Spence were referring to a Rhyphid larva. The whitish larva of *Rhyphus* is "well known and lives in decaying vegetable matter and manure. It is about 10 mm. long, elongate-cylindrical, and devoid of pseudopods. The thoracic segments are longer than broad, and those of the abdomen are separated by intercalary rings, giving the appearance of an increased number of segments. Spiracles are present on the prothoracic and last abdominal segments."

According to Chevrel (1908), a fourth case is recorded by Owen: "A la séance de la Société entomologique de Londres où le Rév. Hope lut le travail dont il a été parlé au commencement de cet historique, R. Owen (1840), dans la discussion qui suivit, dit qu'un malade avait rendu par l'urèthre plusieurs larves de Diptère. Elles n'appartenaient pas aux *Anthomyia* (*Homalomyia*), car elles étaient dépourvues de filaments latéraux." The paper by Hope (1837) was followed by a discussion which was recorded in the *Journal of Proceedings of the Entomological Society* (pp. xlix–l). Professor Owen appears to have been present at this meeting and to have contributed to the discussion. There is no mention, however, of his having referred to any case of urinary myiasis, yet Chevrel could hardly have been present at this meeting in person, because this took place over 70 years before his own paper was written!

Austen (1912) states that the only instance of urethral myiasis in this country of which he was aware was that referred to by Palmer. From an abstract of this author's paper (1900) we learn that at a meeting of the Chelsea Clinical Society "Dr Foster Palmer showed an unusual organism believed to belong to the class of Myriapods, which had been expelled from the urethra of a male patient." Palmer (1901) subsequently reported that the supposed Myriapod was a larva of *Homalomyia scalaris* and "the patient who was present was said to be free from any symptons beyond some thickening in the penile portion of the urethra." No further details of this case are given. Unfortunately Palmer died in 1922, and he does not appear to have published any account of the medical aspects of the case. It seems that he visited the British Museum twice, bringing a single dipterous larva which was identified by Austen. I have failed to obtain further information on the subject.

Considerable difference of opinion would appear to exist with regard to the authenticity of these six cases. Graham-Smith (1913) states that "one case only (of urinary myiasis) has been recorded in this country"; and even this statement takes for granted the authenticity of Dr Palmer's case. Therefore the cases of urinary myiasis which I describe in this paper may be the first two authentic cases of this nature which have been recorded in England.

Records of Urinary Myiasis in other parts of the World

Chevrel (1908)[1] was unable to collect the records of more than 20 cases of urinary myiasis in different parts of the world, although he searched the literature diligently. Of these cases, six were considered authentic, ten probable, and four doubtful. Chevrel's case brought the number of authentic cases up to seven.

Chevrel considered that while the ova might be carried into the urinary passages by sounds and catheters, or by water used for irrigating, they were generally deposited by the adult fly about the meatus urinarius whenever they found favourable conditions, *i.e.* darkness, moisture, oxygen and food. The genitalia, imperfectly protected by clothing, were visited in the early morning by flies attracted by the warmth of the body; if at this time menstruation, recent emission, or discharge from the bladder or urethra had left traces of organic matter about the urinary meatus the flies might easily deposit their eggs there. The victims, deep in sleep, could not protect themselves. Placed under the edge of the prepuce or in the folds of the vulva the eggs so protected and maintained at a high temperature could hatch in a few hours and, being remarkably active, the larvae could creep about and enter the urinary meatus. Owing to the small size of the young larvae they might move about in the mucus without causing tickling sensations and could pass easily into the urethra.

Chevrel's case was that of a paralytic of 55, wife of a farmer, who was left alone all day on a chair which had been converted into a commode by removing the seat and winding the framework with rags. The receptacle for the dejecta was placed on the floor and the flies were free to swarm at will about the buttocks. The woman passed larvae with the urine, daily, from May 19 into July.

Since Chevrel's paper appeared further cases have been recorded by E. F. King (1914) in Virginia and by N. Leon (1921) in Roumania.

History of Dr E. F. King's case in Virginia.

On October 29th, 1914, H. P., man, aged 32, living on a small farm in Virginia, who had been attending Dr King's service at Emergency Hospital, brought to the office an object that he had passed with his urine, which was later identified as a larva of *Fannia scalaris*. He had voided similar objects with the urine on October 19th and 28th, but had not brought them to the doctor, thinking that he would be laughed at.

The man had a chronic posterior urethritis and for some months had been in the habit of urinating in a glass when at home. This glass he kept in a shed at the rear of his house, turned upside down on a shelf, and it was always rinsed after using. He had been using a small syringe of hard rubber for urethral injections and had kept this wrapped in paper and in a closed drawer, so that, apparently, the larvae could not have been in the glass, nor the eggs or larvae in the syringe.

[1] See also Umaña (1915).

About 8 o'clock in the morning, while digging potatoes in his garden, he was seized with an intense desire to urinate, hurried to the shed, felt something pass with the urine and found the larva in the glass. He saw no motion in the larva. King states that he received the specimen two hours later and it was in a fresh condition. According to King, the man had seen no larvae since nor was he able to find any in the faeces after diligent search.

"Contamination probably took place while seated long at stool, the flies being attracted by the presence of a slight urethral discharge. That larvae were voided ten days apart would indicate that they were from different infections. The larvae had evidently penetrated the prostatic urethra, judging by the patient's sensations, though the cystoscopic findings were negative."

King believed that the patient's word could be relied on and that this should be considered as an authentic case of myiasis of the urinary passages.

History of Professor Leon's case in Roumania.

In July, 1920, a student, M. N. T., 22 years old, came to Leon and related that before going to bed he had urinated eleven "worms" which he brought in alcohol. Some days before he had felt at intervals slight tickling sensations accompanied by erections and sometimes by ejaculations. On examination of the specimens under the microscope normal larvae of *Musca domestica*, about 6 mm. long, were recognized. Leon did not think that this case could be a fake, for the young man was a very serious student, robust and in good health. The Professor expressed doubt about the cleanliness of the vessel, but the student assured him that the urine was clear and the smallest foreign body could be seen even at the bottom of the white vessel. Leon then examined the organ to see if by chance flies might not have deposited eggs under the prepuce where the larvae might have made their way into the urethra. The organ was in a state of perfect cleanliness so he had to abandon this hypothesis. The young man said that he had never injected water into the urethral canal, that formerly when attacked by blennorrhagia he had made medicinal injections, but that after his cure (three months previously) he had not made a single further injection. To assure himself that there was no trace of discharge, Leon told the youth to press the organ tightly at the base. As he did this he declared that he suddenly felt a tickling sensation. The organ immediately became erect while the patient, in the Professor's presence, showed pain and evacuated from the urethra with the sperm eight fly larvae resembling in every respect those which he had brought the day before in alcohol. The occurrence left no room for doubt that this was an authentic case of myiasis of the urinary passage.

July, 1920, was very warm at Jassy. The young man said he slept at night without pyjamas, covered only with a sheet which he threw aside at times on account of the extreme heat. The slight discharge still present as the last trace of the blennorrhagia appeared to have been sufficient to attract the flies, which are known to have a strong sense of smell. They had deposited their eggs in the

neighbourhood of the urinary meatus, and larvae had penetrated into the urethra and perhaps even into the bladder.

Leon hoped that the larvae would pupate, but two days later all were dead. He saw the young man again a month later. The student then told him that none of the previous symptoms had recurred. Probably all the larvae had been eliminated naturally.

Two new cases of Urinary Myiasis.

History of Case I. Urinary Myiasis due to the larva of Fannia canicularis *and* Musca domestica.

The patient, a male child, was born on August 30th, 1922, and was breast-fed for the first four or five weeks: when the mother's milk began to disappear it was fed on Glaxo. At this time it was living in lodgings in somewhat unclean surroundings. About April 1st the child suffered from constipation owing to teething, and for no assignable reason began to vomit after each feed. It was then staying at its grandmother's in Longsight, where the premises were more airy and hygienic. Soap injections were given for the constipation and the Virol which the child had been taking was stopped. The vomiting then became less but the child continued to cry just before, but not during or after, the passing of water. The urine had smelt strongly from an early period and now grew offensive. The skin about the genitalia and legs became very inflamed. On August 10th, 1923, after having been taken to the Welfare Centre, the child became very ill, screaming and tossing its head. Convulsions supervened, a private doctor diagnosing "Inflammation of the Brain."

The illness remained "serious" from seven to ten days, and on August 19th a large mass of living maggots and pupae were found on the napkin, "enough being present to cover the palm of the hand." The symptoms now improved and the child seemed brighter, but continued to cry upon passing urine. Under treatment with Hexamine (four grains per day) the child gradually improved, and "only screamed when held out." This improvement lasted till August 28th when the earlier screaming attacks, twitchings and tossings returned. On August 29th the child had another convulsion.

Early in September the child was brought to the Health Clinic by the mother. Several specimens of larvae had been found by her, first in the bed where the child had been lying, then six to seven times in his napkins, and the mother was convinced that the child had passed them in his water. The doctor in charge, Dr King May-Atkinson, did not, at first credit the mother's story, but a napkin was brought which had just been taken off the child, and this was found to contain over 100 specimens. Dr May-Atkinson considers that altogether several hundred must have been passed. The mother was convinced that the larvae were not passed through the rectum, the child being constipated at the time. The child was given Eurotropine and after that passed only dead specimens. When later, in the Baby Hospital, a small sack was fastened over the scrotum, the nature of the myiasis was not definitely determined, since,

by this time, all the larvae appear to have been killed and voided. Several specimens of the larvae (Dipterous) had been brought to the writer for identification early in September. Two distinct species of larvae appeared to be present, namely those of *Fannia canicularis* and of *Musca domestica*. Both species reached the pupal stage, but failed to reach maturity.

History of Case II. Urinary Myiasis due to the larvae of Musca domestica.

Following on Case I, particulars of a second case of urinary myiasis were communicated to me by Professor Peacock, Zoological Department, University College, Dundee. In the early summer of 1920 a few well-grown larvae and many eggs of a Dipteron, preserved in formalin, were brought to him from the Bacteriological Department. They had been received from a doctor in one of the colliery villages about twenty miles from Newcastle-on-Tyne. The following facts were gathered by correspondence with the doctor-in-charge. The specimens had been obtained from a diaper which had been worn for a short time by a sick baby girl and which had become wet with urine but not soiled with faeces. The doctor observed the eggs and larvae upon the diapers. This does not however afford convincing proof that the myiasis was located in the urinary tract for it is possible that, in an anal infection, the eggs and larvae might be dislodged during micturition. That it was a case of a recent chance oviposition upon a diaper or child soiled by urine or faeces, and therefore attractive to flies, is ruled out by the circumstance that well-grown larvae and well-developed eggs were obtained. This points to an infection of some days. Peacock concludes that, notwithstanding the absence of details, this was a genuine case of urinary myiasis. The child was very weakly and died shortly afterwards but how far the myiasis was concerned with its condition of health and subsequent death is not clear.

In a letter to me, Peacock (28. IV. 1926) expressed regret that he had been unable to investigate the case himself "in order to answer satisfactorily the natural questions which arise in one's mind on learning of such a case." He is unable, therefore, to state, with certainty, "how long the condition had obtained or the precise seat of the myiasis, whether urinary, anal or both." The larvae and eggs appear to have been those of *Musca domestica*.

PREVIOUS RECORDS OF CASES OF INTESTINAL MYIASIS IN ENGLAND.

Several instances of myiasis due to larvae in the alimentary canal have been recorded in this country. Most of them appear to be due to the larvae of the lesser house-fly (*Fannia canicularis* L.), and of the latrine fly (*Fannia scalaris* Fab.). Cases of intestinal myiasis due to the former have been described by Jenyns (1839), Cattle (1906), Garood (1910), and Austen (1912), and cases due to the latter are recorded by Stephens (1905), Hewitt (1909), Soltau (1910), and Austen (1912). This author (1912) has also recorded one case due to *Thereva* (? *nobilitata*) larvae, two cases due to *Syrphus* sp. larvae, one case due to *Eristalis tenax* larvae, one due to *Anthomyia radicum* larvae, and two due to

Musca domestica larvae. Various other cases have been recorded from time to time, but no attempt is made to give a complete list in this short paper.

Syrphid larvae appeared to be concerned in the case of intestinal myiasis recorded in the present paper. Judging from the normal mode of life of these larvae it would appear highly improbable that they should be associated with myiasis. Their presence in the human body must, therefore, be regarded as purely accidental. Yet Austen (1912) reports that on two occasions a single Syrphid larva, 9–10 mm. in length, had been submitted to him by medical men, accompanied by the statement that "the creature had been discharged *per rectum* by a patient." We are also told that during some four weeks in September and October, 1907, "a number of larvae of the Drone-Fly were passed *per rectum* by a woman in Hampshire, who had recently arrived from France, where she had eaten a considerable quantity of watercress." According to Dr H. McQuade, Eling Lodge, Totton, Hants, 20–30 larvae (? pupae) "without any tail" were first passed and "after a few days' interval others came singly—all with tails." As was only to be expected, the appearance of the larvae had thrown the patient into a "dreadful state of fear," but it was stated that otherwise she had "suffered no inconvenience."

New case of Intestinal Myiasis.

History of Case III. Intestinal Myiasis due to Syrphid Larvae.

The patient, a woman aged 38, suffered from intense irritation in the anus. This had continued for nearly 12 months before she consulted a doctor. Hot flushes accompanied the irritation, and the stools were very dark, almost black, showing an acid reaction. The bowels were alternately constipated and tending to diarrhoea. There was a slight tenderness over the sigmoid flexure, and scaly patches were evident at the flexures of knee and elbow similar to dry eczema, and at these spots there was a slight irritation. There were no other patches, with the exception of a slight patch at the anus which might be due to friction. The digestion was slightly deranged but this might have been due to nervousness. Dipterous larvae were first found on washing the stool on November 12th, 1923. The stool was passed after taking Santonin. Only one specimen was brought to me for identification, and the structure of the posterior spiracular tubes suggested the probability of its being a Syrphid larva. As there was but one poorly preserved specimen the species could not be determined. Professor Carpenter kindly confirmed the identification.

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(*MS. received for publication* 18. VII. 1926.—Ed.)

[1] Extensive lists of references are given by Chevrel, and some of the writers herein cited.

A LIST OF PARASITIC COPEPODA FOUND AT PLYMOUTH.

WITH A NOTE ON THE BULLA OF *CLAVELLA DEVASTATRIX*.

By W. HAROLD LEIGH-SHARPE, M.Sc. (Lond.).

(With 1 Text-figure.)

Since the publication of a paper by Bassett-Smith (1896, *Journ. Mar. Biol. Assoc.* n.s. iv. 155) a considerable number of new species and other species of parasitic Copepoda has been taken at Plymouth. Bassett-Smith's work forms the basis of this list, but some species are now assigned to other genera, or degraded as synonyms, while in some cases the names of genera are changed owing to preoccupation. Additions have been made by the collections of L. Harrison Matthews and myself.

The names of the collectors have been abbreviated in the appended list as follows: B. = Bassett-Smith, L. = Leigh-Sharpe, M. = Harrison Matthews, S. = Spence Bate, V. = C. D. Vallence.

CALIGIDAE.

Parasite	Author	Collector	Location	Host
Caligus centrodonti	Baird	B.	Tail and fins	*Pagellus centrodontus*
C. curtus	Müller	,,	Mouth	*Gadus morrhua*
,,	,,	,,	Surface of body	*G. minutus*
C. diaphanus	Nordmann	,,	Inner side of operculum	*Trigla hirundo*
,,	,,	B. & M.	,, ,,	*T. cuculus*
C. gurnardi	Krøyer	B.	Pharynx	,,
C. minimus	Otto	,,	Mouth and pharynx	*Labrax lupus*
C. pelamydis	Krøyer	B. & M.	Inner side of operculum	*Scomber scombrus*
C. productus (=*scomberi*)	Dana	B	,, ,,	,,
C. rapax	Milne-Edwards	,,	Scales	*Salmo trutta*
,,	,,	,,	,,	*Gadus morrhua*
,,	,,	,,	,,	*Mugil capito*
,,	,,	M.	,,	*Gobius* sp.
C. zei	Norman & T. Scott	L.	Surface of body	*Zeus faber*
Pseudocaligus brevipedes	(Bassett-Smith)	B.	Pharynx, inner side of operculum	*Onos* [*Motella*] *tricirrata*
Sciaenophilus tenuis	Van Beneden	B.	Inner side of operculum	*Sciaena umbra*
Lepeophtheirus hippoglossi	(Krøyer)	M.	Surface of body	*Hippoglossus vulgaris*
,,	,,	,,	,,	*Rhombus laevis*
L. nordmanni	(Milne-Edwards)	B.	,,	*Orthagoriscus mola*
L. pectoralis	(Müller)	B. & M.	Pectoral fins	*Pleuronectes platessa*
,,	,,	,,	,,	*P. flesus*
,,	,,	B.	,,	*P. limanda*
L. pollachius	Bassett-Smith	B. & M.	Palate, back of tongue	*Gadus pollachius*
,,	,,	,,	,, ,,	*Molva vulgaris*
L. salmonis	(Krøyer)	M.	Surface of body	*Salmo salar*
L. thompsoni	Baird	B. & M.	Gills	*Rhombus maximus*
,,	,,	B. & L.	,,	*R. laevis*

Parasite	Author	Collector	Location	Host
CALIGIDAE.				
Trebius caudatus	Krøyer	B.	Dorsal surface of head and nasal fossae	*Raia batis*
Elytrophora brachyptera	Gerstaecker	,,	Gills	*Thynnus thynnus*
Pandarus bicolor	Leach	,,	Surface of body	*Scyllium catulus*
Cecrops latreillii	,,	,,	Gills	*Orthagoriscus mola*
Orthagoriscicola muricata	(Krøyer)	S.	Surface of body	,,
DICHELESTHIIDAE.				
Lernanthropus kroyeri	van Beneden	B.	Gills	*Labrax lupus*
Hatschekia mulli	(van Beneden)	,,	,,	*Mullus barbatus*
Congericola pallida	van Beneden	B. & M.	—	*Conger conger*
LERNAEIDAE.				
Lernaeocera [*Lernaea*] *branchialis*	(Linnaeus)	B.	Gills	*Gadus morrhua*
,,	,,	,,	,,	*G. aeglefinus*
,,	,,	B. & L.	,,	*G. merlangus*
,,	,,	L.	Buccal cavity	*Callionymus lyra*
,,	,,	B.	Gills	*Labrax lupus*
L. lusci	Bassett-Smith	B. & M.	,,	*Gadus luscus*
Penella sagitta	(Linnaeus)	B.	—	—
Lernaeenicus sprattae	(Sowerby)	,,	Eye	*Clupea harengus*
,,	,,	,,	,,	*C. spratta*
L. encrasicola	(Turton)	,,	Body	*C. alosa*
CHONDRACANTHIDAE.				
Chondracanthus clavatus	Bassett-Smith	B.	Gills	*Pleuronectes microcephalus*
C. cornutus	(Müller)	,,	,,	*P. platessa*
,,	,,	,,	,,	*P. flesus*
,,	,,	,,	,,	*P. megastoma*
C. depressus	T. Scott	M.	,,	*P. flesus*
C. lophii	Johnston	B. L. & M.	Inside operculum and gills	*Lophius piscatorius*
C. merluccii	(Holten)	B.	Mouth	*Merluccius vulgaris*
C. soleae	Krøyer	,,	Gill cavities	*Solea vulgaris*
C. zei	De la Roche	B. L. & M.	Inner side of operculum	*Zeus faber*
Medesicaste asellinum	(Linnaeus)	B.	Gills	*Trigla gurnardus*
,,	,,	,,	,,	*T. cuculus*
,,	,,	,,	,,	*T. hirundo*
LERNAEOPODIDAE				
Salmincola salmonea	(Gissler)	B.	Gills	*Salmo salar*
Lernaeopoda galei	Krøyer	B. & L.	Cloaca, claspers	*Galeus vulgaris*
L. globosa	Leigh-Sharpe	L.	Nasal fossae	*Scyllium canicula*
L. mustelicola	,,	,,	Cloaca	*Mustelus vulgaris*
L. scyllicola	,,	,,	Cloaca, claspers	*Scyllium canicula*
Clavella devastatrix	,,	L. & M.	Gills, pharynx, inside of operculum	*Gadus merlangus*
C. iadda	,,	L.	Skin, fins, tail, anus	*G. morrhua*
C. invicta	,,	M.	—	*G. pollachius*
C. sciatherica	,,	L.	Buccal cavity, pharynx	*G. morrhua*
Clavellisa emarginata	(Krøyer)	B.	Gill-rakers	*Clupea alosa*
C. scombri	(Kurz)	M.	Gill-arches	*Scomber scombrus*
Clavellopsis paradoxa	(van Beneden)	B.	Gills	,,

LERNAEOPODIDAE.

Parasite	Author	Collector	Location	Host
C.(?) quadrata	(Bassett-Smith)	,,	Gill-rakers	*Callionymus lyra*
Brachiella bispinosa	Nordmann	,,	,,	*Trigla gurnardus*
,,	,,	,,	,,	*T. cuculus*
,,	,,	,,	,,	*T. lyra*
B. merluccii	Bassett-Smith	,,	Points of gill-rakers	*Merluccius vulgaris*
B. obesa	(Krøyer)	M.	Gill arches	*Trigla gurnardus*
B. thynni	Cuvier	B.	Behind pectoral fins	*Thynnus thynnus*
B. triglae	Claus	,,	Gills	*Trigla gurnardus*
,,	,,	,,	,,	*T. cuculus*
,,	,,	,,	,,	*T. hirundo*
Epibrachiella [Thysanote] impudica	(Nordmann)	B. & M.	Inside of operculum	*Trigla gurnardus*
,,	,,	,,		*T. cuculus*
,,	,,	,,		*T. hirundo*
Parabrachiella insidiosa	(Heller)	,,	Gill-rays	*Merluccius vulgaris*

HERPYLLOBIIDAE.

Hedyphanella superba	Leigh-Sharpe	L.	Dorsal surface	*Gattyana cirrosa*
Phallusiella psalliota	,,	,,	,,	*Lagisca floccosa*
P. vera	,,	,,	,,	*Malmgrenia castanea*
Sarsilenium crassirostris	(M. Sars)	V.	,,	*Evarne impar*

NOTE I. *Parasitology*, XVIII. 153, line 23. The implied resemblance is between the second maxillae of *Nicothoë* and the first maxillae of *Lernaeopoda*.

NOTE II. ON THE BULLA OF *CLAVELLA DEVASTATRIX*. In *Parasitology*, XVII. 197, the new species *Clavella devastatrix* was but imperfectly described since the available specimens lacked an undamaged bulla. I am now able to give a figure (Fig. 1) of a complete bulla. The bulla is ellipsoidal with its minor axis in continuity with the manubrium; cf. XVII. 196, Fig. 1.

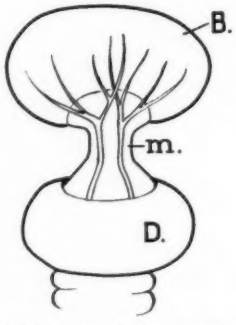

Fig. 1. *Clavella devastatrix* ♀. *B* = bulla; *m* = manubrium; *D.* = disc.

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ERRATA. VOL. XVIII.

P. 151, line 9. *Read* biramous *for* uniramous (see Fig. 4).
P. 153, line 15. *Delete* the words in parenthesis.
P. 276, line 6. *Read* median *for* medium.

THE TREMATODES OF *CORVUS INSOLENS* (A BURMESE HOUSE-CROW), WITH A DESCRIPTION OF FOUR NEW SPECIES.

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(With 7 Figures.)

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Introduction.

The trematodes described in this paper were collected by Miss Reynolds and myself from *Corvus insolens*, a Burmese house-crow, specimens of which contained many parasites of different species, all being minute except in two cases. They were obtained by washing the intestines after opening them in luke-warm water in a large glass basin, whence they were removed by means of a pipette, being readily identified owing to their slight movements. Those occurring in the liver were obtained by teasing that organ in luke-warm water. Table I records the results of the examination of five crows for parasites. I am much indebted to Miss Reynolds for the help she gave me in placing the material she collected at my disposal.

Table I.

Crow No.	Parasite	Organ whence obtained	Number collected
1	*Platynosomum acuminatum* Nicoll, 1915	Liver	1
	Lyperosomum kakea n.sp.	,,	16
2	*Echinochasmus corvus* n.sp.	Intestine	90
	Phaneropsolus insolens n.sp.	,,	40
3	*Echinochasmus corvus* n.sp.	Intestine	80
4	*Echinochasmus corvus* n.sp.	Intestine	3
5	*Stephanoprora reynoldi* n.sp.	Intestine	1

Echinochasmus corvus n.sp. (Figs. 1, 2.)

The worms are broad posteriorly and taper anteriorly, measuring 1·06–1·08 × 0·465–0·49 mm. At the anterior end is a collar and no separate neck portion is visible. The whole body is covered with very delicate cuticle, so that even in the living worm, slight pressure renders it possible to study

most of the internal anatomy. The cuticle is beset with oblique rows of spines directed posteriorly. These spines are very numerous at the anterior end as far as the ventral sucker, posterior to which they grow sparser, disappearing at the hind end of the posterior testis. The oral sucker is situated at the end of the anterior conical portion of the body and measures 0·076–0·086 mm. in diameter. The pre-pharynx is short (0·027 mm.). The oral sucker and pre-pharynx are surrounded by a kidney-shaped collar opening ventrally. It has 24 spines, disposed in one row which is broken dorsally by a short space: of these 3 ventral are "Eckstacheln" and 9 dorsal "Randstacheln" on each side. The spines get larger dorsally, the biggest being those facing the dorsal diastema and the smallest the "Eckstacheln" on the ventral side. The largest measures 0·047 × 0·018 mm. and the smallest 0·0225 × 0·009 mm. The ventral sucker is situated at about one-third the distance from the anterior end and measures 0·13–0·14 mm. in diameter, the ratio between the two suckers being approximately 1:2. Posterior to the pre-pharynx is the pharynx measuring 0·058 mm. It is followed by an oesophagus which passes posteriorly and bifurcates into two intestinal caeca anterior to the ventral sucker. These are simple and pass along the sides posteriorly to the end of the body.

The testes are situated in the posterior region of the body, in the central line, one behind the other and are separated from the posterior end by a broad band of vitellaria. The anterior testis is transversely oval, with an entire margin and measures 0·26 × 0·15 mm. The posterior testis lies immediately behind it and is somewhat round, but its anterior margin is flattened owing to its contact with the anterior testis, so that it appears to be bluntly triangular. It measures 0·23 × 0·175 mm. The cirrus-sac lies on the dorsal side of the ventral sucker, in the central line, and extends posteriorly almost to the posterior margin of the ventral sucker. It opens to the exterior by means of the genital opening situated anterior to the ventral sucker, between it and the intestinal fork. Nearly two-thirds of the posterior portion of the body is occupied by the vesicula seminalis. The pars prostatica and the ductus ejaculatorius are very small. The copulatory organ is not very powerful.

The ovary is situated immediately anterior to the testes, on the right side of the middle line. It is oval and measures 0·1–0·13 × 0·08–0·105 mm. The receptaculum seminis is situated on its inner side and is round. Laurer's canal present. The shell-gland lies in the centre in front of the anterior testis. The uterus is very small and lies between the anterior testis and the ventral sucker. It passes dorsally to the latter and opens to the exterior by means of the genital pore. It contains very few eggs, the maximum number counted in one specimen being only eight. The eggs are oval, operculated, with brown shell, and measure 0·07–0·085 × 0·045–0·06 mm. The vitellaria consist of large rounded follicles, situated dorsally along the sides of the body. The follicles on each side meet centrally in front of the ventral sucker anteriorly and behind the testes posteriorly. They extend from the hind end of the body to slightly anterior to the intestinal fork: in no case do the follicles reach the

pharynx. Stout transverse vitelline ducts are seen between the ovary and the anterior testis, which meet together in the central line and pour their contents into the shell-gland.

The genus *Echinochasmus* was founded by Dietz (1909) to include the species *E. beleocephalus* (v. Linstow 1873), *E. coaxatus* Dietz 1909, *E. perfoliatus* (Ratz 1908) and *E. euryporus* (Looss 1896). Odhner (1910) included in it the species *liliputans* (Looss 1896), *africanus* (Stiles 1901) and *bursicola* (Looss 1899), and the genus *Episthmium* Lühe 1909. Lühe (1909) distinguishes the genus *Episthmium* from *Echinochasmus* only on the ground of the extension of the vitellaria, which in the former do not extend more anteriorly to the posterior border of the ventral sucker, while in the latter they extend as far as the pharynx. This is not a very good point of difference and I agree with Odhner in eliminating the genus *Episthmium*. Nicoll also appears to hold the same opinion since the species he described (1914) as *prosthovitellatus* was included in the genus *Echinochasmus* although the vitellaria in that case extend as far as the pharynx. Such a minute difference in the extension of the vitellaria might serve as a good specific distinction, but is poor for distinguishing one genus from another. The genus *Episthmium* therefore passes into synonymy under the genus *Echinochasmus*. Johnston (1917) described *E. tenuicoli*, Kotlan (1922) described *E. amphibolus* and Baer (1922) *E. botauri*. Of these, the species *coaxatus*, *beleocephalus*, *euryporus*, *perfoliatus*, *tenuicoli*, *amphibolus*, *liliputans* and *botauri* differ from the species under consideration in the following respects: (1) The vitellaria being posterior to the ventral sucker, (2) the cirrus-sac being either very small or extending only as far as the centre of the ventral sucker, (3) the ratio of the suckers being very different. *E. bursicola* differs from it in the general dimensions of the body, the testes being almost in the mid-body, the ratio of the suckers being 3: 5 and the cirrus-sac being very small. *E. africanus* differs in size, in the form of the testes, and in the eggs being much bigger. It comes much nearer to *E. prosthovitellatus* among the existing species, but differs from it also in the general dimensions of the body, the ratio of the suckers being 1: 2 instead of 1 : 3, the vitellaria not reaching anteriorly as far as the pharynx, the posterior testis being entire instead of slightly notched and the spines not extending as far as the end of the body, but disappearing at the hind border of the posterior testis. These points of difference being of sufficient importance to justify the creation of a new species, I propose to name it *Echinochasmus corvus*.

Specific diagnosis. Body broad behind and tapering anteriorly. Cuticle with spines as far as the posterior border of the testes. Collar with 24 spines: 3 + 3 "Eckstacheln" and 9 + 9 "Randstacheln." Ratio of suckers 1 : 2. Vitellaria not reaching pharynx anteriorly. Testes in posterior part, entire. Eggs 0·07–0·085 × 0·045–0·06 mm.

Host—*Corvus insolens* (intestine).

Locality—Rangoon.

NOTE ON AN ABNORMAL FORM OF *E. corvus* n.sp. (Fig. 3.)

One of about a dozen specimens, mounted *in toto*, showed interesting deviations from the type as follows: (*a*) There was but one testis, rather transversely oval, entire, situated in the posterior part of the body, and measuring 0·18 × 0·155 mm. The presence of one testis is unknown in Distomata: the only genus which is characterised by the possession of one testis being *Asymphylodera* Looss 1899. (*b*) On the left side the caecum extends as far as the posterior end of the body, but on the right side it only extends posteriorly as far as the centre of the ovary. (*c*) The vitellaria on the left side extend from the posterior end to slightly anterior to the intestinal fork, but on the right side they extend anteriorly only to the level of the ovary. (*d*) Measurements: body 0·76 × 0·355 mm., oral sucker 0·07 mm. in diameter, ventral sucker 0·13 mm. in diameter, pre-pharynx 0·07 mm., oesophagus 0·07 mm. in length, and ovary 0·08 × 0·07 mm. The uterus contains only one egg. The cuticular as well as the collar spines are as in the type specimen.

STEPHANOPRORA REYNOLDI n.sp. (Figs. 4, 5.)

Only one specimen of this species was found in the intestine of *Corvus insolens* by Miss Reynolds (after whom the species is named) while working in the Zoological Laboratory of the University of Rangoon. An excellent mount was obtained, so the minutest details were clearly discernible.

The worm is elongated, being almost cylindrical from the level of the ventral sucker to the anterior testis and tapering towards the ends. At the anterior end is a collar and the portion following it as far as the ventral sucker appears neck-like. It measures 4·2 mm. in breadth, the maximum being reached at the level of the ventral sucker. The whole body is covered with fine, transparent cuticle which is beset with backwardly directed spines in the anterior region of the body. These spines are very numerous in the neck region, but grow sparser behind the level of the ventral sucker, disappearing at the posterior level of the anterior testis.

The oral sucker, situate at the extreme anterior end, appears slightly drawn out posteriorly. It measures 0·21 × 0·68 mm. and is surrounded by a kidney-shaped collar which is discontinuous ventrally. The collar bears 22 spines arranged in one row that is discontinuous dorsally. Of these the two smallest ventral spines are the "Eckstacheln" on each side, and there are 9 "Randstacheln," the former being situated opposite the latter. The largest spine measures 0·0407 × 0·019 mm. and the smallest 0·025 × 0·009 mm. The pre-pharynx is short, measuring 0·14 mm. in diameter. Immediately behind the pharynx is an oesophagus of moderate length, 0·2 mm. This divides, anteriorly to the ventral sucker, into two simple intestinal caeca passing posteriorly almost to the end of the body. The excretory pore, which leads into an excretory bladder, is situated at the posterior end of the body. The bladder has a long stem which bifurcates, forming two arms behind the posterior testis.

The nervous system consists of two short transverse bands fused in the centre on the antero-dorsal side of the pharynx. The anterior band gives out two nerves to the front of the body, while the posterior one gives two long nerves which pass posteriorly.

The testes are two oval bodies, with entire margins, situated one behind the other, in the centre of the body, the actual central line of the body passing between them, so that one testis lies in the anterior half while the other lies in the posterior half of the body. The anterior testis is rounded and measures 0·39 × 0·33 mm., while the posterior testis is more elongated and measures 0·50 × 0·33 mm. From their anterior ends issue two fine vasa efferentia which pass forward and meet on the left side slightly behind the ventral sucker to form a short common duct, the vas deferens. This passes forward and enters the cirrus-sac situated on the left side of the ventral sucker and extending from the intestinal fork to its posterior end. It is pear-shaped, broad anteriorly and tapering posteriorly and contains a large two-lobed vesicula seminalis occupying slightly more than half its posterior portion. The ductus ejaculatorius and pars prostatica are small. The copulatory organ is not well developed.

The ovary is an oval body, situated anterior to the testes, slightly to the right of the middle line and measuring 0·15 × 0·115 mm. Its margin is entire, like that of the testes. Posterior to it and slightly towards the left side is situated the receptaculum seminis, and posterior thereto, in the central line, is a diffuse shell-gland. Laurer's canal present. The uterus is small and its coils extend only between the anterior testis and the ventral sucker. It contains a few ova measuring 0·056–0·0895 × 0·031–0·049 mm. The vitellaria consist of large follicles extending from the centre of the anterior testis to the posterior end along the sides of the body. The follicles on each side in the posterior region approach each other very closely. Vitelline ducts are seen passing forward from each gland at the sides of the anterior testis. Immediately in front of the latter they meet to form a large yolk reservoir which sends out a short vitelline duct to open into the ootype surrounded by the shell-gland.

Dietz (1909) founded the genus *Mesorchis* and included in it the species *pseudoechinatus* (Olss. 1876), *polycestus* Dietz 1909, *denticulatus* (Rud. 1802), *conciliatus* Dietz 1909, and *pendulus* (Looss 1899). Odhner (1911) placed the genera *Mesorchis* Dietz 1909 and *Monilifer* Dietz 1909 under the genus *Stephanoprora*. I am in complete agreement with him since the differences between Dietz's two genera are insignificant, *Mesorchis* having an elongated body with antero-posteriorly elongated testes, while *Monilifer* is a small form having transversely elongated testes. These differences might serve to differentiate species but do not afford means of separating genera. Subsequently Linton (1910) added *urna* and Lutz (1924) *singularis* and *pitangi*, the last being described as *Monilifer pitangi*. The genera *Monilifer* (now *Stephanoprora*) and *Echinochasmus* are very closely related, differing only by the extension of the vitellaria. Lutz was probably led to include his species in the genus *Monilifer* because of the number of spines on the head-collar being 22, but this cannot be regarded as a good generic character, for species with varying numbers of spines are recorded in the same genus. We do not find the same variability with regard to the extension of the vitellaria,

all other species included under *Stephanoprora* having their vitellaria extending only as far as the testes. The species *pitangi*, having these glands extending as far as the intestinal fork, cannot be included under *Stephanoprora* Odhner 1910; it is best accommodated under *Echinochasmus* Dietz 1909.

The description of *Stephanoprora urna* was not accessible to me in India. Among other species, *pseudoechinatus*, *denticulatus*, *pendulus*, and *singularis* can be separated from the species under discussion on account of the vitellaria being more posteriorly disposed, either not reaching as far as the testes or extending only as far as the centre of the posterior testis, the testes being more posterior, the cirrus-sac extending at the most up to the centre of the ventral sucker and the ratio between the two suckers being different. *Spinosa*, *ornata* and *polycestus* have the vitellaria extending as far as the anterior border of the posterior testis, the cirrus-sac only reaching as far as the centre of the ventral sucker, the testes in the case of the first two being transversely elongated or notched and in the case of the last one more anteriorly disposed, and the ratio of the suckers being 1 : 3. It comes much nearer to *conciliatus*, agreeing with it in the extent of the vitellaria, the ratio of the suckers and the number and disposition of the spines on the head-collar; but it differs in being much bigger, the testes being more anterior, the cirrus-sac extending as far as the posterior border of the ventral sucker and the host being different. Therefore it is necessary to create a new species for which I propose the name *Stephanoprora reynoldi*.

Specific diagnosis. Body elongated. Cuticular spines disappearing at the posterior margin of anterior testis. Collar with 22 spines: 4 "Eckstacheln" and 18 "Randstacheln." The "Eckstacheln" opposite the "Randstacheln." Testes in mid-body. Cirrus-sac extending to posterior border of ventral sucker, situated on the left. Vitellaria extend anteriorly to the centre of anterior testis. Eggs 0·056–0·089 × 0·031–0·049 mm.

Host—*Corvus insolens* (intestine).

Locality—Rangoon.

Phaneropsolus insolens n.sp. (Fig. 6.)

The worms are pear-shaped, broad posteriorly and tapering anteriorly, and measure 0·585–0·73 × 0·29–0·365 mm., the greatest breadth being at the level of the testes. The body is covered with very thin and transparent cuticle so that under slight pressure most of the anatomy can be studied under a low magnification. The cuticle is entirely covered by transverse rows of backwardly directed spines.

The mouth is subterminal on the ventral side of the body and is surrounded by a circular oral sucker measuring 0·115 × 0·1 mm. It is followed by a globular, muscular pharynx 0·03–0·035 mm. The oesophagus is very short; it soon divides into two short intestinal caeca passing postero-laterally and ending somewhat anterior to the testes. The ventral sucker is smaller than the

oral and is situated in the centre of the body, posterior to the intestinal fork. It is circular and measures about 0·1 mm. in diameter. The ratio between the two suckers is 10 : 11.

The excretory pore lies at the hind end of the body and leads into a V-shaped bladder whose arms are very broad and diverge to the sides and end slightly behind the testes.

The testes are oval bodies, with entire margins and measuring 0·97–0·12 × 0·07–0·093 mm. They lie symmetrically, but their position with regard to the ventral sucker shows some variation, this depending upon the degree of contraction of the body. Sometimes they lie in line with the ventral sucker, sometimes postero-lateral to it and not infrequently they lie completely behind it, but in most specimens they lie postero-laterally to the ventral sucker. Two small vasa efferentia arise from the anterior end of the testes; they meet on the dorsal side of the ventral sucker and enter the cirrus-sac. This varies in shape, being sometimes zigzag and often horse-shoe-like. On the dorsal side it partly overlaps the ventral sucker and partly it is anterior to it, between it and the intestinal fork. At its posterior end is a large vesicula seminalis and following it is the portion of the pars prostatica. The ductus ejaculatorius is small and it is followed by a fairly long muscular penis which is capable of being protruded through the genital pore situated immediately anterior to the ventral sucker, on the left side of the middle line.

The ovary lies to the right of the ventral sucker and is often overlapped by the right testis. It is oval and measures 0·6–0·7 × 0·04–0·05 mm. The shell-gland lies behind the ventral sucker, in the central line. The receptaculum seminis varies in size; it lies on the inner side of the right testis. Laurer's canal present. The uterus is long and coils in the posterior part of the body behind the testes; it opens to the exterior by a common genital pore. The eggs are brown, operculated, 0·018–0·022 × 0·097–0·0105 mm. The vitellaria are situated at the sides of the intestinal caeca. The follicles are small, 8–12 on each side and sometimes a few of them overlap the intestinal caeca. The vitelline duct from each gland extends over the intestinal caecum and the ventral sucker and meets with its fellow on the other side behind the latter to form a reservoir from which a duct leads into the shell-gland.

The present form with small, pear-shaped body, V-shaped excretory bladder, short intestinal caeca, testes symmetrical and postero-lateral to the ventral sucker, vitellaria at the sides of the intestinal caeca, long cirrus-sac and the whole body covered with spines, belongs to the genus *Phaneropsolus*. This genus was founded by Looss (1899) to include *longipenis* Looss 1899, *microon* (Rud. 1819), *orbicularis* (Des. 1850), *oviformis* (Poir. 1886), and *sigmoides* Looss 1899. All of these species, *microon* excepted, differ from mine in the opening of the cirrus-sac being in the neighbourhood of the pharynx, the cirrus-sac extending anterior to the intestinal fork and the caeca ending comparatively anterior to the ventral sucker. In addition to these, *P. longipenis* and *P. orbicularis* have the testes anterior to the ventral

sucker. *P. oviformis* has the ovary behind the ventral sucker. It comes much nearer to *P. microon* but differs from it in the genital pore being near the ventral sucker, the size of the cirrus-sac not being S-shaped, the ventral sucker being comparatively bigger. Moreover, the ovary and the receptaculum seminis in the case of *P. microon* are not observed. Therefore it is necessary to create a new species for which I propose the name *Phaneropsolus insolens*.

Specific diagnosis. Body pear-shaped, covered with spines. Oral sucker bigger than ventral. Intestinal caeca passing posteriorly to the level of the anterior border of ventral sucker. Testes postero-lateral to ventral sucker. Cirrus-sac not extending anterior to intestinal fork. Genital pore anterior to ventral sucker, to the left of central line. Ovary to the right of ventral sucker. Vitellaria lateral to intestinal caeca. Eggs 0·06–0·07 × 0·04–0·05 mm.

Host—*Corvus insolens* (intestine).

Locality—Rangoon.

Lyperosomum kakea n.sp. (Fig. 7.)

The worms are elongated, tapering at both ends and measuring in a well-extended specimen 3·36 × 0·33 mm., the greatest breadth being at the level of the ventral sucker. The whole body is covered with a thin cuticle devoid of any armature. Living specimens were sufficiently transparent for the study of the internal anatomy under low magnification, with slight pressure from a cover-slip.

The oral sucker is terminal, measuring 0·13 × 0·15 mm. There is no pre-pharynx. The pharynx is immediately behind the oral sucker and is globular, measuring 0·6 mm. in diameter. It is followed by a moderately long oesophagus which forks, forming two simple intestinal caeca passing to the posterior end along the sides of the body. The ventral sucker is circular and is situated at one-fifth the distance from the anterior end of the body, measuring 0·2 mm. in diameter. The ratio of the oral to the ventral sucker is 2 : 3.

The excretory system is typical of the genus.

The testes are two oval bodies lying one behind the other some distance behind the ventral sucker. They are placed centrally with their axes oblique to the length of the body and measure 0·15–0·18 × 0·12–0·125 mm. Vasa efferentia arise from these and pass anteriorly along the sides of the ventral sucker and meet some distance anterior to it to form a vas deferens. This enters the cirrus-sac, lying centrally about 0·28 mm. anterior to the ventral sucker. It is pear-shaped and opens to the exterior by means of the genital pore situated some distance behind the pharynx. At its posterior end is seen the coiled vesicula seminalis. The pars prostatica, the ductus ejaculatorius and the cirrus are small.

The ovary is an ovoid body lying behind the testes, in the central line and measuring 0·165 × 0·12 mm. Its longer axis is transverse to the length of the body. Immediately behind it lies the receptaculum seminis which is smaller and

circular. Laurer's canal present. The shell-gland is central, behind the ovary. The coils of the uterus entirely fill up the posterior part of the body behind the ovary and anteriorly their course is zigzag between the ovary and the posterior testis, and the anterior testis and the ventral sucker. Ultimately the coils pass anteriorly dorsal to the ventral sucker and continue as the vagina which opens to the exterior by means of the genital pore. The vitellaria are small and consist of a few follicles extending to a short distance, 0·33–0·43 mm., behind to the ovary. Two short vitelline ducts are seen behind the shell-gland; they meet centrally and send a common duct to enter it. The eggs are oval, operculated, measuring 0·028–0·03 × 0·016–0·018 mm.

Among the genera of Dicrocoelinae Looss 1899, my species with paired and symmetrical vitellaria, much elongated body which is not broader than thick and testes one behind the other, can be placed in the genus *Lyperosomum* Looss 1899. This genus was founded by Looss (1899) to include the species *porrectum* (Braun 1899), *plesiostomum* (Linstow 1883), *longicauda* (Rud. 1809), *strigosum* Looss 1899 and *clathratum* (Deslongchamp 1824), the last of which was removed by Looss (1907) to the genus *Platynosomum*. Later on were added *lobatum* (Railliet 1900), and *olssoni* (Railliet 1900). Braun (1901) added *corrigia*, *salebrosum*, *rudectum*. Von Linstow (1906) added *squamatum*, but it was later shown by Skrjabin (1913) not to belong to this genus. Skrjabin (1913) added *filiformi*. Nicoll (1914) added *scitulum* and *direptum*. Johnston (1917) added *parvum*, *megastomum* and *harrisoni*, and Travassos (1917) added *obliquum*, *transversum*, *rarum*, *lari* and *sinuosum*. Travassos's paper was not accessible to me in India. Among the remaining species of *Lyperosomum* my species comes much nearer to *Lyperosomum lobatum* (Railliet 1900). It *resembles* it in having genital glands entire, ovary smaller than testes, both testes being anterior to ovary, vitellaria posterior to ovary and testes being in anterior third of body. It *differs* from it in size, having a relatively much smaller oral sucker situated terminally instead of subterminally, the ovary oval instead of circular, its long axis being transverse to the long axis of the body, ventral sucker having no ear-shaped appendage, cirrus-sac being much anterior to the ventral sucker and the vitellaria not being so far behind the ovary. These differences suffice for the creation of a new species which I propose to name *Lyperosomum kakea*.

Specific diagnosis. Body elongated, tapering at both ends, broadest at the level of the ventral sucker. Ventral sucker larger than oral. Testes oval, one behind the other, somewhat posterior to ventral sucker, their long axis being oblique to the axis of the body. Ovary behind testes, its long axis being transverse. Cirrus-sac ends some distance anterior to testes. Genital pore near pharynx. Vitellaria a short distance behind ovary. Eggs 0·028–0·03 × 0·016–0·018 mm.

Host—*Corvus insolens* (liver).

Locality—Rangoon.

Platynosomum acuminatum Nicoll 1915.

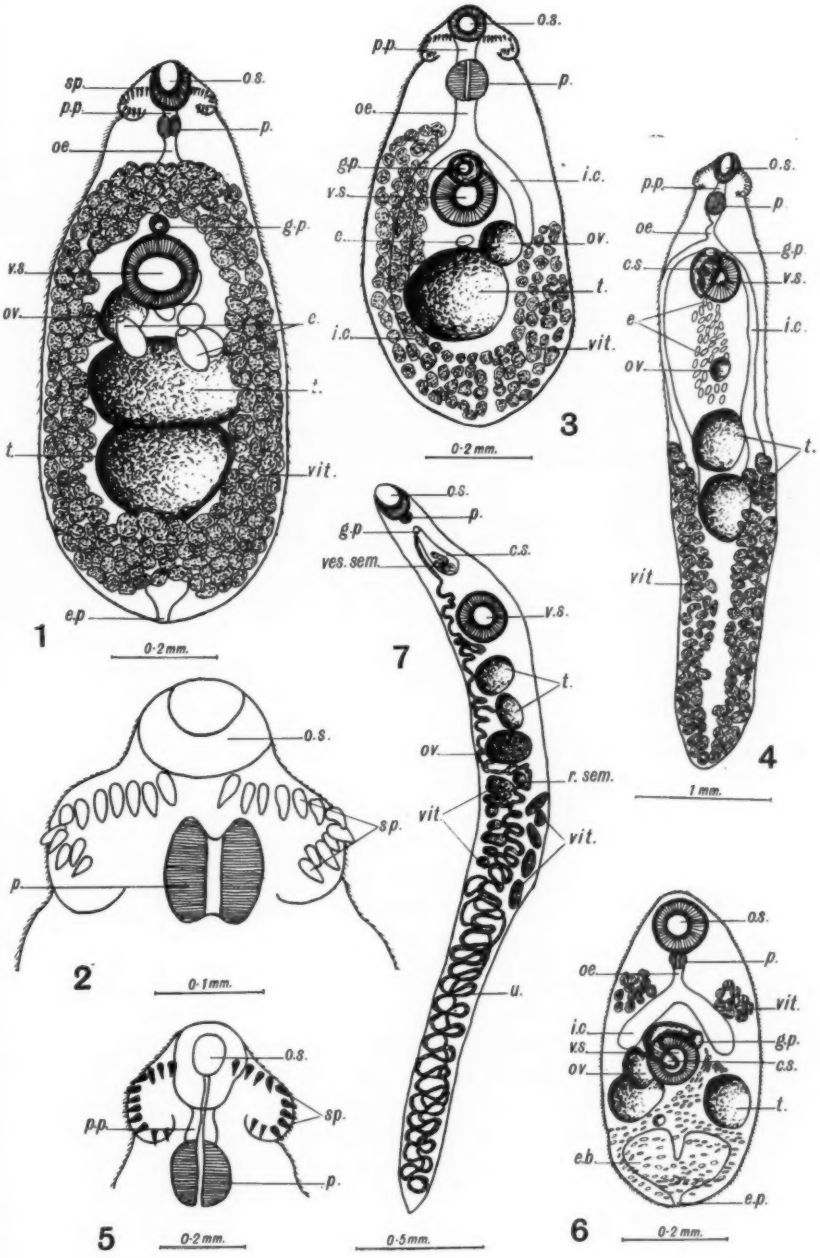
Only one specimen of this species was obtained from the liver of *Corvus insolens*. It agrees in most respects with *Platynosomum acuminatum* Nicoll 1915. The only points of difference are the dimensions of the body and the vitellaria being some distance behind the testes and not extending as much posteriorly. These differences are insufficient for the creation of a new species.

EXPLANATION OF FIGURES ON OPPOSITE PAGE.

Fig. 1. *Echinochasmus corvus* n.sp.
Fig. 2. „ „ anterior end.
Fig. 3. „ „ abnormal form.
Fig. 4. *Stephanoprora reynoldi* n.sp.
Fig. 5. „ „ anterior end.
Fig. 6. *Phaneropsolus insolens* n.sp.
Fig. 7. *Lyperosomum kakea* n.sp.

EXPLANATION OF LETTERING.

c.s.—cirrus-sac.
e.—eggs.
e.b.—excretory bladder.
e.p.—excretory pore.
g.p.—genital pore.
i.c.—intestinal caecum.
oe.—oesophagus.
o.s.—oral sucker.
ov.—ovary.
p.—pharynx.
p.p.—pre-pharynx.
r.sem.—receptaculum seminis.
sp.—spine.
t.—testis.
u.—uterus.
v.s.—ventral sucker.
ves.sem.—vesicula seminalis.
vit.—vitellaria.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ON THE NUTRITION OF THE MALE OF *LERNAEOPODA SCYLLICOLA*.

By PETER GRAY.

(With 4 Figures.)

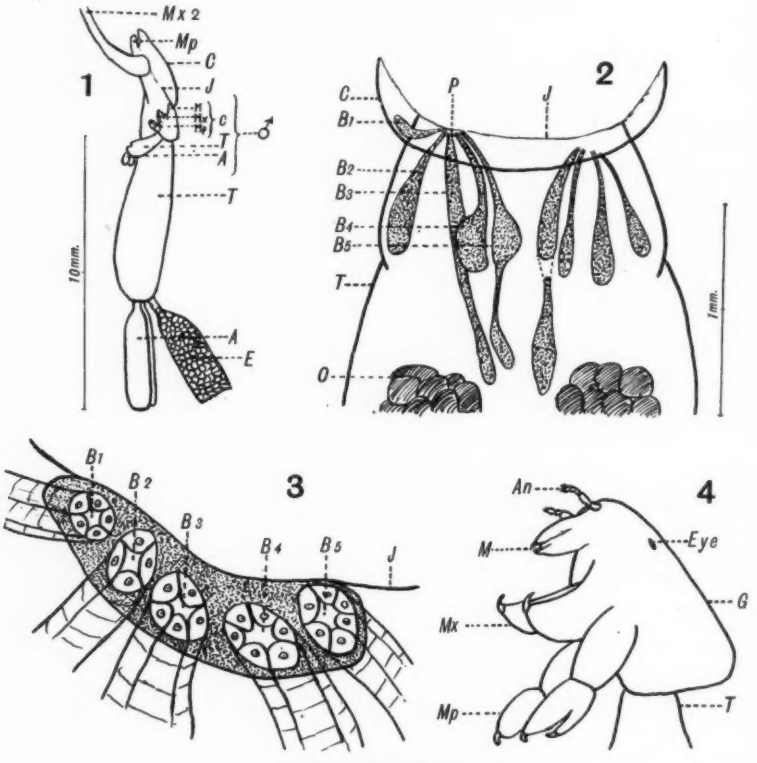
Leigh-Sharpe (1918, *Parasitology*, xi. p. 24) states that the alimentary canal of the male has no visible contents and quotes Wilson (1915) to the effect that there is never an anus. He (Leigh-Sharpe) makes three suggestions: (i) that the male never feeds, (ii) that it feeds on the spermatozoa of the dogfish or (iii) on the eggs of the nematode which infests the latter. It is unlikely that the copepod is capable of completely digesting the chitinous case of the eggs in a canal which Wilson (*loc. cit.*) states to be sparingly furnished with glands; but if there is to be no debris all material taken in must be completely digested and absorbed. If the male never feeds the mouth would degenerate as rapidly as the anus; the mouth and oesophagus are both well developed. That spermatozoa form the food is a suggestion which cannot be disproved except by observation of the living animal.

At all events it seems that fluid or semi-fluid nutriment probably partially predigested is taken into the canal. Working on this assumption I searched for glands in the neighbourhood of the mouth which would assist in external digestion but could find no trace.

I next turned my attention to the shoulder of the female, on which the male normally rests (Fig. 1), and saw in an unstained specimen faint indications of what appeared to be a system of glands. The specimen was then stained for 36 hours in Grenacher's alcoholic borax carmine and differentiated in $\frac{1}{2}$ per cent. hydrochloric acid for a week. The glands I had noticed took the stain very deeply and upon mounting in balsam appeared as dark red against a light scarlet ground.

Ten elongated sacks, five upon each side of the middle line, occupy a position between the junction of the cephalo-thorax and trunk and the anterior margin of the ovary (Fig. 2). Their anterior ends, which are very narrow, open into a pouch (Fig. 3) whose upper wall is the flap of the cephalo-thorax and which thus communicates with the surface exactly at the junction of the trunk and cephalo-thorax. The surface opening is completely protected by the overlapping of the cephalo-thorax. These bodies differ in size and shape but agree in having a blind posterior end more or less clavate, in tapering postero-anteriorly and in the granular aspect of their walls. Those upon the left side are far more developed than those upon the right: I cannot make out a surface opening on the right.

I beg to suggest that these sacks are used for the production and storage of food for the male and I therefore propose the name "bromatophores" (*βρῶμα*—food). (I do not consider that they are concerned in external digestion for reason (4) given below.)



Lernaeopoda scyllicola.

Fig. 1. Lateral view of ♀ with ♂ resting in normal position.
Fig. 2. Anterior portion of trunk and base of cephalo-thorax of ♀, dorsal aspect.
Fig. 3. Details of the region *P* in Fig. 2.
Fig. 4. Cephalo-thorax of ♂, latero-ventral aspect.

A. Abdominal appendage. *An*. Antennules. *B*1–*B*5. Bromatophores. *C*. Cephalo-thorax. *E*. Egg string. *J*. Junction of cephalo-thorax and trunk. *M*. Mouth. *Mp*. Maxillipede. *Mx*. Maxilla. *O*. Ovary. *P*. Pouch into which the bromatophores open. *T*. Trunk.

In support of this proposition I would draw attention to the following facts.

(1) That fluid or gelatinous nutriment is taken into the alimentary canal of the male.

The secretion of the bromatophores would obviously be either fluid or gelatinous.

(2) That the bromatophores open into a pouch at the junction of the trunk and cephalo-thorax towards the "shoulder."

The males of this genus are always taken near this position and can only move with difficulty (Fig. 1).

(3) The development of the bromatophores upon the left is great; those upon the right do not even open on to the surface.

The three recorded specimens, and the two I myself have taken, of *L. scyllicola* (male) were all upon the left shoulder.

(4) The mouth of the male (Fig. 4) is at the end of a mouth-cone of some length for which no function has been previously suggested.

The surface opening of the bromatophores is covered by an overlapping of the cephalo-thorax and could not be reached by a sessile-mouthed male.

(5) If for any reason the mouth of the bromatophores became inaccessible to the male we should expect that he would endeavour to cut or scratch an opening to it. The "tumours" figured by Leigh-Sharpe (1919, *Parasitology*, XI. p. 263) upon the left shoulders of females of this species are possibly the result of such conduct.

(6) Bromatophores are found only in the female.

(*MS. received for publication* 10. IX. 1926.—Ed.)

CALIGUS ZEI NORMAN AND T. SCOTT 1906 (CRUSTACEA: COPEPODA), WITH A REVISION OF THE APPENDAGES.

By C. L. OAKLEY.

From the Chelsea Polytechnic, London.

(With 4 Figures.)

Habitat and record. The animal under consideration, a copepod of the Family Caligidae, has up to the present received three notices: by Norman and T. Scott (1906), A. Scott (1907), and T. and A. Scott (1913). (For further particulars see References at end of this paper, p. 409.) Norman and Scott stated that "the specimens were taken forty years ago on the dory by Laughrin, and by him sent to A. M. N." Consequently, the specimens were forty years old before they were described, which would, even in the absence of other reasons, excuse a little scepticism as to the description. Scott gives a bare record of capture, with a copy of Norman and Scott's diagrams. These diagrams and the original of Norman and Scott are republished by Scott and Scott with the addition of a few errors. Considering these facts, and also that no satisfactory description is given of the appendages of the male, or of the maxillae or swimming legs of the female, and that the animal is very common, occurring on nearly every dory, I feel that there is some justification for a further description.

The specimens on which this account is based were taken from the body-surface of a John Dory (*Zeus faber*) caught at Plymouth in May, 1926. They included both sexes, and were examined both while living and immediately after death.

MALE. (Fig. 1.)

Length 7·7–8 mm.

Carapace sub-orbicular, margins only slightly arcuate, posterior notches fairly deep. Cephalic area forms two-thirds of the carapace, and is furnished with seven pairs of appendages and the sternal fork; thoracic area forms the remaining third, is transversely orbicular, and provided with the first three pairs of swimming legs. Eyes paired, fused together in the middle line, lenses pointing outwards and slightly forwards. Eyes situate dorsal to mouth tube.

The *free* (4th) *Thoracic segment* is very small, half as long as broad, and bears the fourth pair of swimming legs.

The *Genital Segment*, which, according to Wilson (1907, 1908) is formed by the complete fusion of the fifth and sixth thoracic segments, is oblong, longer

than broad, about equal in length to the two following segments; it shows a slight constriction anteriorly which may be the joint between the fifth and sixth segments (this does not seem to have been Wilson's original opinion, but is rather borne out by his figure of the male of *Homoiotes palliata*, 1905). It bears at its posterior end, ventrally the fifth, and dorsally the sixth pair of swimming legs. (See Fig. 2.)

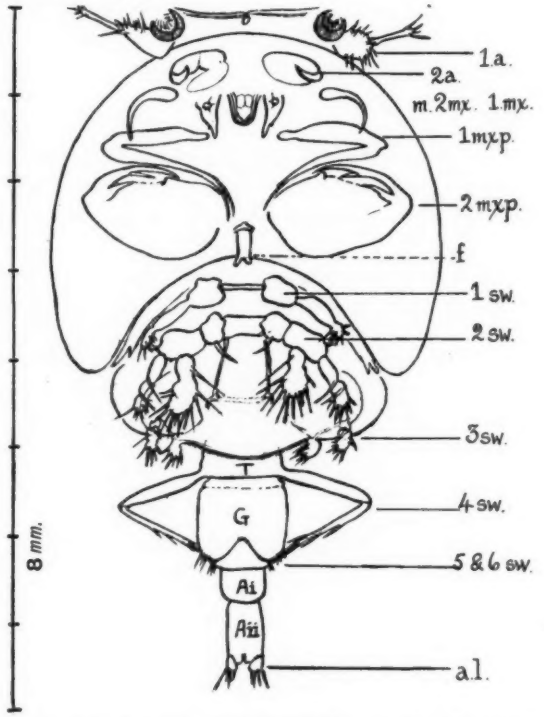


Fig. 1. *Caligus zei* ♂, in ventral aspect, showing appendages *in situ*. *T.* = free thoracic segment; *G.* = genital segment; *Ai.*, *Aii.* = abdominal segments; 1*a.* = first antenna; 2*a.* = second antenna; *m.* = mandible; 1*mx.* = first maxilla; 2*mx.* = second maxilla; 1*mxp.* = first maxillipede; 2*mxp.* = second maxillipede; *f.* = furca; 1, 2, 3, 4, 5, 6 *sw.* = swimming legs; *a.l.* = anal laminae.

Of the two *abdominal segments* which follow, the first is small, square, about half as wide as the genital segment, and bears no appendages; the second twice as long as the preceding and equal to it in width, bears at its posterior end the anal laminae, which are small, square, flattened dorsiventrally, and bear four plumose setae.

The **Appendages** are thirteen in number all paired.

The *first antennae* (Fig. 3 *a*) are unusually long. The basal joints are fused in the middle line to form the frontal plates, in the centre of which appear the median incision and the frontal sucker so important in the chalimus stage.

The frontal plates and the lunules (sucking discs) which they bear are moderately large. The second joint is about twice as long as broad, and bears anteriorly many plumose setae; the terminal joint is longer than the preceding, about five times as long as broad, and bears one seta posteriorly, and eight setae terminally.

The *second antennae* (Fig. 2 *A*) are two-jointed, the basal joint being thick and strong, and provided with a heart-shaped thickening in the chitin against which the strongly recurved unciform terminal joint bites.

The *first maxillae* (Fig. 2 *E*) are sharply uncinate, and placed at the lateral margins of the carapace.

The *second maxillae* (Fig. 2 *B*) are placed laterally to the mouth tube, and consist of a strong tapering *exopodite* furnished laterally with two spinous processes (recalling the bifurcate appearance of this appendage in *Lepeophtheirus*); the *endopodite* is represented by a small circular chitinous plate bearing three setae.

The *mandibles* (Fig. 2 *G*) lie wholly within the mouth tube, and are three-jointed, the terminal joint being provided with twelve recurved teeth on its inner margin.

The *first maxillipedes* (Fig. 2 *C*) are slender and two-jointed; the terminal joint about as long as the basal, and ending in two long setae, the more medial the longer.

The *second maxillipedes* (Fig. 2 *F*) are very strong; the enlarged basal joint is furnished medially with a blunt process, against which the uncinate terminal joint, which is provided with a long accessory spine, can bite.

The *sternal fork* or *furca* (Fig. 4 *C*) is rather small, consisting of an oblong basal plate, and two small square, nearly parallel limbs.

The *mouth tube* (Fig. 2 *G*) is very complicated, and can best be understood from the figure.

The *swimming legs* are six pairs.

The *first pair* (Fig. 3 *d*) is uniramous and three-jointed. The basal joint is nearly twice as long as broad, bears a seta posteriorly, and a plumose seta at its anterolateral corner. The second joint is twice as long as the first, provided at its anterolateral corner with a seta, and posteriorly fringed with small setae. The terminal joint is slightly smaller than the first, and is furnished posteriorly with three plumose setae, and terminally with three spines, the third of which is very long, and the remaining two bifurcated (a condition found by Wilson (1905) in several American species, *e.g. C. schistonyx*, *C. latifrons* and *C. chelifer*, but not yet recorded in any British species. See Fig. 3 *c*).

The *second pair* (Fig. 3 *e*) is biramous. Of the two basal joints the first is sub-quadrilateral, furnished with a plumose seta posteriorly; the second is oblong and massive, about twice the length of the preceding furnished anterolaterally with a spine, and posteriorly with a fringe of small setae. The *exopodite* is three-jointed, the first joint being equal in length to the two others; the second joint is square, bearing two backwardly directed spines, one at each

anterior corner, and a posterior plumose seta. The terminal joint is rather more circular, and bears a blunted spine and eight plumose setae. The *endopodite*

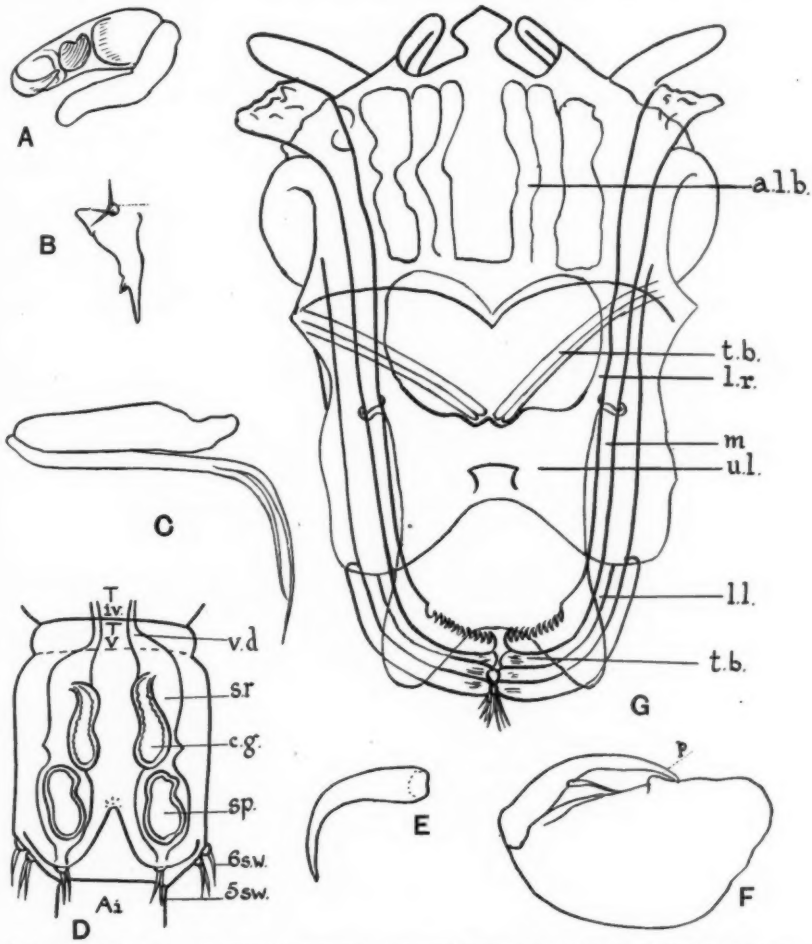


Fig. 2. *Caligus zei* ♂. *A* = second antennae; *B* = second maxilla; *C* = first maxillipede; *D* = genital segment of male in ventral aspect; *T*iv. = fourth thoracic segment; *T*v. = fifth thoracic segment (?); *v.d.* = vas deferens; *s.r.* = spermatophore receptacle; *c.g.* = cement gland; *sp.* = spermatophore; *5sw.* = fifth pair of swimming legs; *6sw.* = sixth pair of swimming legs; *Ai* = first abdominal segment; *E* = first maxilla; *F* = second maxillipede; *p.* blunt process; *G* = mouth tube under a high magnification; *a.l.b.* = accessory longitudinal bars; *m.* = mandible; *l.r.* = main longitudinal rod; *t.b.* = transverse bars; *u.l.* = upper lip; *l.l.* = lower lip.

is also three-jointed, the first two joints about equal in size, the terminal somewhat smaller. The first and second bear a long posterior plumose seta, the terminal seven plumose setae.

The *third pair* (Fig. 3 *f*) is biramous. The basal joints are enlarged and fused together in the middle line to form the powerful swimming "apron." The *endopodite* is one-jointed, furnished with one large and seven smaller plumose setae. The *exopodite* is two-jointed, the first rather the larger, provided with a strong two-jointed hook, a plumose seta medially and a spine laterally. The terminal joint is circular and bears lateromedially one small and two large plumose setae, and one small and two large spines.

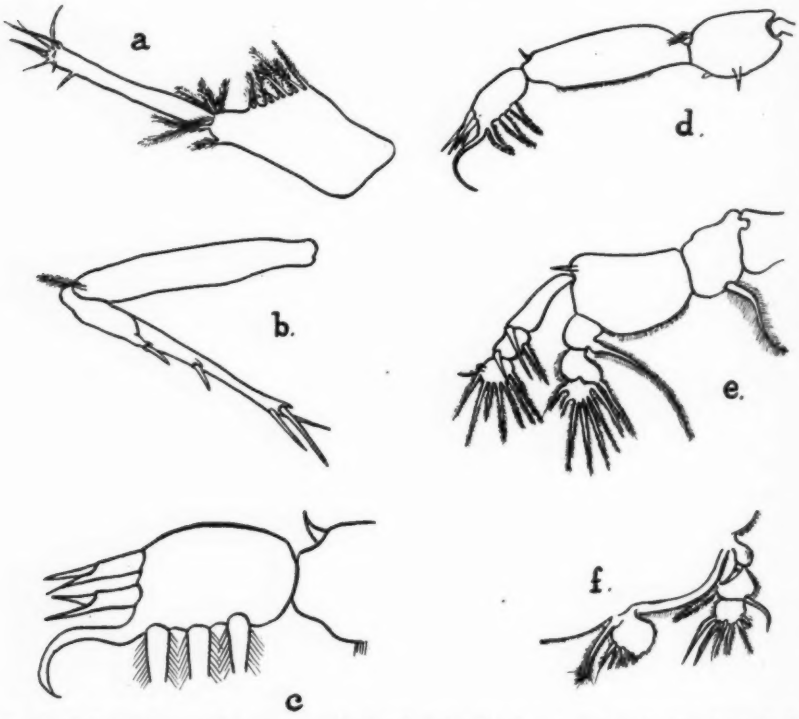


Fig. 3. *Caligus zei* ♂. *a*=first antenna; *b*=fourth swimming leg; *c*=enlarged view of terminal joint of first swimming leg to show bifurcate setae; *d*=first swimming leg; *e*=second swimming leg; *f*=third swimming leg.

The *fourth pair* (Fig. 3 *b*) is uniramous and three-jointed. The basal joint is about equal in length to the other two, rather slender, and bears a plumose seta terminally; the second joint is small and terminates in a spine; the third is about twice as long as the preceding, articulates obliquely with it, and is provided with a posterolateral and one small and three large terminal spines.

The *fifth pair* is vestigial, and is represented by one pair of unjointed knobs each provided with two setae, on the posterior ventral corners of the genital segment (Fig. 2 *D*, 5*sw*.).

The *sixth pair* in the form of two pairs of unjointed knobs, provided with three setae, occur at the posterior dorsal corners of the genital segment (Fig. 2 *D*, 6*sw*.).

The *anal laminae* have already been described.

FEMALE. (Fig. 4 *A*.)

Length 7·5–7·8 mm.

The *carapace* is of the same form as in the male: the *free thoracic segment*, however, is relatively even smaller, about four times as broad as long. The *genital segment* is bulky, square, and about as wide as the carapace; it bears the sixth pair of swimming legs, and the *egg-strings* characteristic of the Copepoda, which are about as long as the animal's body; *eggs* fairly large.

The *abdomen* is one-jointed, about one-third the width of the genital segment, and two-fifths of its length. It bears anal laminae much larger than those of the male.

The *furca* (Fig. 4 *D*) is much larger than that of the male; the legs are much longer than the basal plate, and diverge to a moderate extent. It is remarkable that the furca of the female is attached to the carapace posterior to the hinge between the cephalic and thoracic areas; while that of the male is attached anterior to it.

Appendages. Only such as differ markedly from those of the male are here described.

The *second antennae* (Fig. 4 *E*) are two-jointed, the basal joint being inflated and provided with a strong curved posterior spine; the terminal joint is longer than in the male, sharply uncinate, but cannot bite against the basal joint.

The *first maxillae* (Fig. 4 *F*) are almost straight, and much slenderer than in the male.

The *second maxillae* are unprovided with lateral spines.

The *first maxillipedes* are similar to those of the male, but their terminal spines are provided with a serrated fringe (as in *C. chelifer*).

The *second maxillipedes* (Fig. 4 *G*) are much slenderer than in the male, the basal joint being much less inflated, and lacking a blunt process; the accessory spine on the terminal joint is also much smaller. There is no sign of a *fifth pair* of swimming legs.

The *sixth pair* of legs is even smaller than in the male, consisting of a pair of knobs, each provided with two setae. (See Fig. 4 *B*.)

Specific Characters common to both sexes. Parasitic on *Zeus faber*; small free segment; unusually long antennae; frontal plates and lunules smaller than in most species; bifurcate spines on terminal joint of first pair of swimming legs; unusual arrangement of spines and setae on other legs; mandibles toothed along inner margin only.

Specific Characters of the male. Free segment small; genital segment showing marked anterior constriction, and both fifth and sixth pairs of swimming

legs; abdomen two-jointed; limbs of furca very small; lateral spines on the second maxillae; blunt process on second maxillipede.

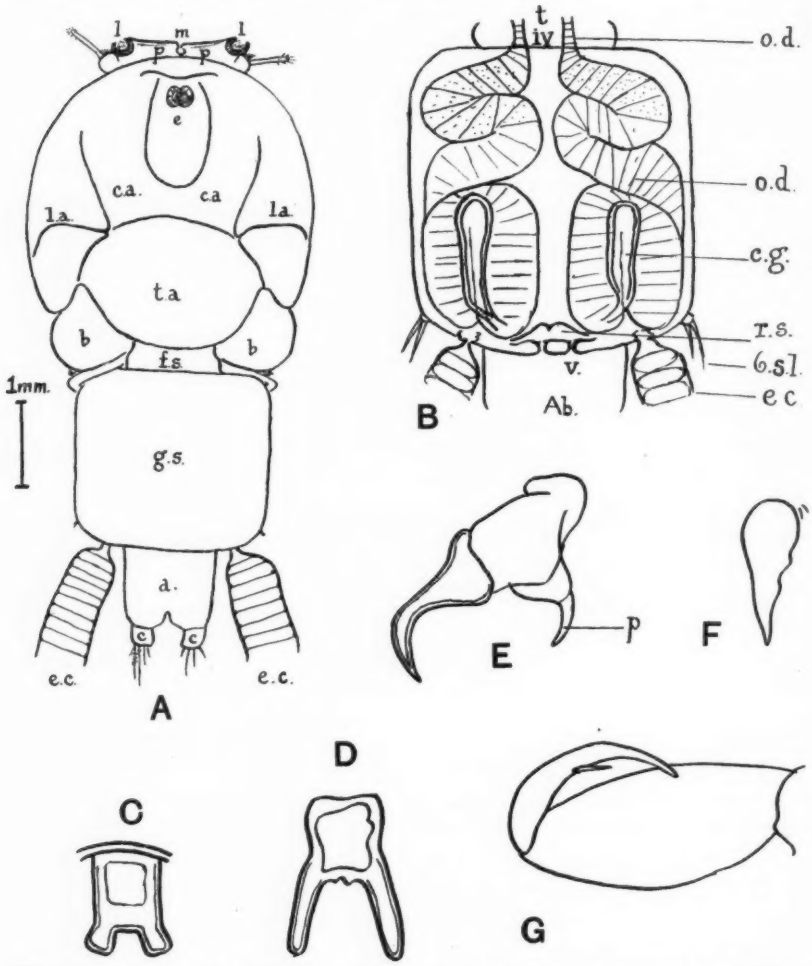


Fig. 4. *Caligus zei* ♀. *A* = in dorsal aspect to show grooving of the carapace and segmentation; *l.* = lunules; *m.* = median incision; *p.* = frontal plates; *e.* = eyes; *c.a.* = cephalic area; *l.a.* = lateral area; *t.a.* = thoracic area; *b.* = basal joints of third swimming legs; *f.s.* = free thoracic segment; *g.s.* = genital segment; *a.* = abdomen; *c.* = anal laminae; *e.c.* = egg-strings; *B* = genital segment in ventral aspect; *t.*iv. = fourth thoracic segment; *o.d.* = oviduct; *c.g.* = cement gland; *r.s.* = receptaculum seminis; *v.* = vulva; 6.*s.l.* = sixth swimming legs; *e.c.* = egg-strings; *Ab.* = abdomen; *C* = furca of ♂; *D* = furca of ♀; *E* = second antenna of ♀; *p.* = posterior spine; *F* = first maxilla of ♀; *G* = second maxillipede of ♀.

Specific Characters of the female. Free segment very small, genital segment very large and square, showing only sixth swimming legs; abdomen one-

jointed; furca large, attached posterior to cephalothoracic hinge; fringe on spines of the first maxillipede.

In my opinion this species forms a connecting link between the genera *Caligus* and *Lepeophtheirus*; the small size of the frontal plates and lunules, the attempt at a bifurcation of the second maxillae, the fact that there are no signs of teeth on the outer margin of the mandibles, and the prominence of both fifth and sixth swimming legs all strongly favour this conclusion.

Acknowledgments. I have to thank Mr W. H. Leigh-Sharpe for his help and many valuable suggestions. Furthermore, I am indebted to Miss F. Hargreaves for preparing the illustrations which accompany this paper.

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AN EXPERIMENTAL STUDY OF TICK PARALYSIS IN AUSTRALIA.

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(With 2 Text-figures.)

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INTRODUCTION.

A PARALYSIS of man and animals associated with presence of ticks has long been known to occur both in Australia and other countries. The species of tick implicated in the causation of tick paralysis differs in the several countries, but the nature of the disease in all cases presents certain features in common. Attention was first drawn to the condition in Australia by Backhouse (1843), who ascribed deaths in sheep and calves to the effects produced by ticks; later, Bancroft (1884) described in some detail the symptoms shown by naturally affected dogs and mentioned the effects seen in human beings.

In *Australia* cases of tick paralysis in man have been recorded by Cleland (1912), Eaton (1913), and Strickland (1915). Dodd (1921) first produced tick paralysis in the dog experimentally with *Ixodes holocyclus* and Ferguson (1924) records a fatal case of paralysis in a child in which this tick was present. Suspicion does not appear to attach to any other species in Australia, though in many of the cases of tick paralysis of man no specific determination of the tick present was made.

In *Canada*, Todd (1912), Temple (1912) and Bishopp and King (1913) directed attention to the occurrence of tick paralysis in man, and *Dermacentor venustus* fell under suspicion. Hadwen (1914) described the symptoms of tick paralysis in sheep caused by *D. venustus* ♀♀, while Hadwen and Nuttall (1915) were able to produce paralysis of the dog experimentally with a single female

D. venustus brought to England from Canada. Bruce (1922) has recorded cases in cattle where *D. venustus* was again regarded as the responsible agent. In one case in man, however, Todd (1915) only found *Haemaphysalis punctata* var. *cinnabarina* present and this tick must therefore be regarded with suspicion.

In *South Africa*, Malley (1904) recorded tick paralysis in sheep due to *Ixodes pilosus*, while Blane and Caminopteros (1924) describe a similar condition in sheep in *Crete*. In this case *I. ricinus* appears to be the principal cause, though *Haemaphysalis punctata* may also prove of some importance.

Thus tick paralysis is known to occur in four continents, Australia, North America, Africa and Europe, while four species of ticks are regarded as the causal agents, namely, *I. holocyclus*, *I. pilosus*, *I. ricinus*, and *D. venustus*. *Haemaphysalis punctata* var. *cinnabarina* and *Haemaphysalis punctata* have not been shown to cause paralysis but are suspect.

I. SYMPTOMS.

In *Australia*, Dodd (1921) demonstrated that a single tick was able to cause fatal paralysis in the dog, and showed that symptoms did not develop till five days after the attachment of the tick. The symptoms were those of motor paralysis first affecting the hind limbs, then ascending rapidly to involve the forelimbs, head and neck. Death resulted from respiratory paralysis. In man it was also observed that one tick could cause fatal paralysis, the general course of the disease corresponding to that in the dog. It is not easy to obtain authentic evidence as to the symptoms in foals, calves and sheep, though it would appear that these animals are affected. Mr Haywood, late manager of the Grafton Experiment Farm, has informed me that he has seen cases of paralysis in sheep, the symptoms resembling those in dogs and cats. Although the ticks were removed as soon as the lambs were seen to be affected these usually died. He has also seen many cases in fowls, calves and pigs.

In *Canada*, Hadwen (1914) observed in experimental cases of tick paralysis in sheep that symptoms appeared 6–7 days after the attachment of ticks, the onset coinciding with the attainment of the final stage of rapid engorgement of the female tick. Hadwen and Nuttall (1915) also observed this in the dog. The symptoms of tick paralysis of both man and dog in Canada are similar to those seen in Australia, but Canadian cases are perhaps less severe since more recoveries apparently follow upon the removal of the ticks.

In *South Africa* the affected animals first show paresis of the hind quarters followed by complete paralysis. A single tick is stated to cause as serious an attack as that induced by a number of ticks.

In *Crete* a similar train of symptoms is observed, and in cases where ticks are removed in the early stages of the disease recovery frequently follows, but when advanced symptoms have developed death usually occurs in spite of their removal.

Personal Observations in Australia.

The writer has been able to observe many experimental cases of tick paralysis in the dog, in all cases due to *I. holocyclus*. These ticks were reared in the laboratory, mostly from immature stages recovered from *Perameles nasuta* (the Bandicoot) captured near Sydney.

In no case have diagnostic symptoms been observed before the fifth day after the attachment of the tick. For four days the animals appeared normal but for slight local reaction and swelling at the site of attachment of the tick. A few dogs exhibit slight languor before definite symptoms develop, and there may be an appreciable rise in temperature, though this is also inconstant. The appetite usually is unaffected. Thus there are no definite premonitory symptoms whereby one may be warned of the onset of an attack, which is usually sudden and perhaps in all dogs characterised by an affection of the hind limbs.

It should be emphasised that the period elapsing between the attachment of the tick and the onset of symptoms is inconstant—we shall see that it corresponds to the stage of the tick's engorgement, rather than to a period of time. In experimental dogs the first definite symptoms may not appear until thirteen days after the attachment of the ticks. The incubative period, though not wholly dependent on the weather, tends to be longer in winter than summer.

Where a definite rise in temperature occurs this may signify an impending attack, but the first constant symptom is a slight incoordination affecting the hind quarters. Whether ticks are removed at this stage or not the incoordination rapidly becomes more marked, so that in 2–3 hours the dog may be unable to stand. Movements of the limbs may be vigorous but they are incoordinate. Later the motor disturbance ascends rapidly to involve the muscles of the fore limbs so that the dog cannot raise itself and lies extended; respiration is slowed and embarrassed, all the accessory muscles being brought into play. On taking food or drink there is nearly always violent retching, but vomition is difficult. In fatal cases the muscles of the head, neck, tongue and larynx become affected and swallowing is difficult. Vomition is now always a marked and most distressing feature and may follow the administration of warm normal saline. Nevertheless some movement of the limbs is usually possible, so that the dog makes feeble convulsive movements, especially during the paroxysms induced by the respiratory embarrassment. The few reflexes that can be elicited in the dog are modified or abolished early in the disease, while the corneal reflex may be slower than normal, this even in a dog that does not show distinct paresis. The pupil may be widely dilated although reacting to light till shortly before death.

It should be mentioned that early in the disease the muscles innervated from all levels of the cord are affected as shown by the dog being unable to bark or masticate hard food, though still able to stand.

In contrast to the severity of the motor disturbance other symptoms are but slight: while there is often an initial fever, the temperature in most severe cases soon falls to below normal. Sensibility appears little affected, and dogs in a very advanced stage of paresis appreciate stimuli, though able to make only the feeblest motor response. Dying dogs remain mentally bright almost to the end; they follow one with the eyes and appreciate remarks even though unable to raise their heads. It is striking that the cardiac function is but little disturbed, the heart may maintain fair strength and rhythm till shortly before death. In one case the heart continued to beat strongly for 20 minutes after natural respiration had ceased.

Defaecation and urination do not appear to be much affected while animals are able to stand. When unable to stand it is difficult to determine whether the retention which subsequently occurs is due to voluntary abstention such as is frequently seen in dogs unable to stand from other causes.

Death in all cases appears to be due to respiratory paralysis. It may be stated that the more rapid the onset of symptoms after the attachment of the tick, the more severe will the attack be, and the more rapid the fatal termination. Moreover, the severity of the respiratory symptoms appears to run parallel to the degree of paresis affecting the limbs. In no experimental cases have dogs recovered after the paretic condition had become so marked that they were unable to stand, though recovery undoubtedly occurs in some cases. This affords a contrast to Hadwen and Nuttall's case where the dog recovered though the paralytic condition had been such that it was unable to lift its head.

The following cases illustrate the onset and course of the disease. In all cases by "tick," the adult *I. holocyclus* ♀ is meant. The male seldom attaches itself to a host and it is of no pathogenic importance.

Case A. Dog 4, Fox Terrier, weight 9 kilos. Two ticks, 27–29 days after emergence, were placed on the dog, one tick being put in each ear.

2nd day. Ticks little changed in appearance.

3rd day. Ticks slightly swollen dorso-ventrally.

4th day. Ticks slightly increased in length.

5th day. Ticks noticeably larger.

6th day. One tick decidedly increased in size had reached final rapid stage of engorgement. Dog bright and normal.

7th day. Dog at 9 a.m. distinctly affected, unable to stand. Temp. subnormal, 100·4° F. Resp. 12, laboured. Dog struggling as if from anoxaemia. Large tick killed by ammonia but did not withdraw. Dog disposed to eat but had difficulty in swallowing. Strychnine nitrate gr. $\frac{1}{50}$ given. Respiration appeared to become easier. Temperature at midday 101·7° F. Dog vomited during afternoon. 5 p.m. Temp. 101·6° F. Resp. 16. Second tick now removed.

8th day. Dog weaker. Resp. 11, very laboured. Pulse 130. On drinking water commenced to vomit, suffering great respiratory distress. Urine escaped involuntarily. Saline enemata given.

9th day. Dog very weak, gasping at each respiration. Temp. 96° F. Resp. 10. Pulse 96. Died, respiration ceasing suddenly, while heart was still beating strongly.

Autopsy. Muscles cyanotic. Marked oedema of cardiac half of stomach, but no other naked eye lesions. Brain and spinal cord showed no microscopic lesions.

Urine analysis. Bright yellow, acid, no albumen, sugar or bile present.

In this case the ticks engorged normally and the onset of the attack synchronised with the final rapid stage of engorgement. There was also a characteristic absence of premonitory symptoms. *This case illustrates the usual mode of onset and course of the disease.*

Case B. Dog 2, weight 10½ kilos. One tick, 7–9 days after emergence, was placed in the dog's ear and attached itself in a few minutes. Temp. 102·8° F. Resp. 24. Pulse 110. Weather cold, falling at night to 6° C. Tick engorged slowly till 11th day.

12th day. Dog's temperature 105·1° F. Animal bright.

13th day. Dog showed distinct incoordination of hind limbs, and tended to fall on turning or stopping suddenly. Dog no longer barked, but was cheerful and active. Temp. 103·9° F. Tick now about half gorged.

14th day. Dog cannot stand. Appetite good. Temp. 99·4° F. Resp. 18, laboured. Pulse 140, irregular. Reflexes could be obtained though modified. Sensation undiminished. Temperature rose in evening to 100·6° F.

15th day. Temperature 99·6° F. Resp. 12. Pulse 144. Fore limbs could be moved feebly. Hind legs completely paralysed. Pupil dilated but still reacted to strong light. Corneal reflex abolished. Mucous membranes cyanotic. Tick nearing complete engorgement.

16th day. Temperature could not be registered. Swallowing very difficult. Tick showed no noticeable increase in size.

17th day. Temp. below 95° F. Resp. 10. Pulse 70. Tick showed little increase in size.

18th day. Temp. below 95° F. Resp. 6. Pulse 40. Mucous membranes cyanotic, limbs motionless, animal comatose. Died at 1 p.m. Tick still attached.

Autopsy. Superficial vessels congested. Muscles cyanotic. No lesions in abdominal viscera. Congestion of lungs. No naked eye lesions in brain and spinal cord other than congestion of vessels.

Urine analysis. Pale green. Acid. No evidence of acetone, albumen, bile sugar or blood.

In connection with this case note: (*a*) the long period elapsing between the attachment of the tick and the onset of the attack corresponding to the slow engorgement of the tick; (*b*) the prolonged course of the disease, death not occurring till five days after the onset, the tick not having been removed.

Case C. Dog 5. Wire-haired terrier, weight 8 kilos. A tick, 56 days after emergence, attached itself above the dog's eye, and became very slowly engorged.

10th day. Tick showed distinct increase in size.

11th day. Tick not noticeably larger.

12th day. Dog's temperature rose to 104·3° F., but animal bright and cheerful, though showing slight incoordination of hind quarters. Tick killed at 3 p.m. 4 p.m. dog ate raw meat and then vomited; incoordination more distinct. Pulse and Resp. normal. Dog not distressed.

13th day. Temp. 104·3° F. Resp. 20. Pulse 118. Incoordination more pronounced, though dog still able to stand. Vomited when over-disturbed. Refused food. Ptosis of eyelid and corneal reflex delayed on right side. Dog's pulse and respiration did not become alarming, no treatment given other than A. Hydrocyan. Dil. to stop vomition. In the evening Temp. 102·8° F. Resp. 20. Pulse 112.

14th day. Temp. 102·8° F. Pulse 112. Resp. 21. Dog brighter, though some incoordination present. Vomited violently without having taken food or drink. Sight apparently affected. Ptosis of right eyelid still present. In the evening vomited, the heart being slowed to 62, soon recovering to 112 per minute.

15th day. Dog much brighter and stronger. No incoordination. Slight tendency to vomit. Temp. 103·2° F. Resp. 21. Pulse 114.

16th day. Dog apparently normal.

This case, illustrating a non-fatal attack, is of interest because of the (*a*) slow onset of symptoms, this corresponding to the prolonged period of the tick's engorgement; (*b*) the mild course run, dependent on the same factor; (*c*) paresis of limbs not being marked, while respiration was not seriously embarrassed. Vomition was a distressing feature. Temperature never subnormal, this corresponding to mild nature of the attack.

Similarly, in the case of another animal, Dog 13, paresis never became severe, respiration was not seriously embarrassed and the temperature did not fall below normal. The animal, however, could not bark and the pupil became widely dilated.

Case D. Dog 16, aged 4 months, weight 3·5 kilos. Four ticks were allowed to attach themselves in the dog's ears, where they became engorged normally. Dog appeared well till 6th day, when there was slight fever but no other symptoms were shown. The ticks appeared to be approaching the final rapid stage of engorgement. Two hours after first being seen, the animal again appeared normal. Two hours later, at 2 p.m., the dog showed distinct incoordination and, though it tried to run about, it fell repeatedly. The ticks were now removed surgically. At 5 p.m. the dog was still able to stand, and ate a little meat. At 9 p.m. temp. 102·8° F., dog unable to stand; respiration embarrassed and stertorous.

7th day. Animal lying extended, gasping at each inspiration. Temp. 97·5° F. Died during the night.

Autopsy. No naked eye lesions.

Note the small size and youth of the dog, that nevertheless symptoms only developed on the 6th day after the 4 ticks became attached.

In the case of another animal (Dog 15), weighing under 4 kilos and under 6 months old, upon which 4 ticks were gorging, no symptoms developed till the evening of the 5–6th day.

Case E. Dog 9. One tick, 27 days after emergence, became attached in the dog's ear. On the 6th day the tick appeared to be at the rapid stage of engorgement. The dog had been perfectly well but in the evening appeared somewhat quieter than usual, its temperature being 103·1° F. On running about, very slight incoordination of the hind quarters could be detected. On the 7th day, in the morning, the tick was found to have dropped off fully gorged. Dog showed slightly more distinct incoordination but could still run about. Temp. 101·6 F. At midday incoordination was much more pronounced, and at 7 p.m. the dog could not stand. Death occurred on the morning of the 8th day.

This case is striking in that at the time the tick had become fully gorged, the dog only showed slight symptoms, yet died 24 hours later. Note also the fall in temperature on 7th day. *This case illustrates yet another variation in the onset of the attack.*

II. PATHOLOGY.

Previous observers have recorded that there are practically no specific naked eye lesions. Dodd found little abnormality of the organs in dogs, while Ferguson, in sections of the brain and spinal cord of a child, failed to find any signs of degeneration of the neurones in the anterior horns, which, as will be shown, are probably the seat of the tick-derived toxin's action.

Personal Observations.

In experimental cases in the dog no specific naked eye lesions were seen, though there was frequently some congestion of the lungs. Notwithstanding the constant vomiting, gastritis was not observed. Hoping that histological examination of the nervous tissues would reveal more definite lesions, sections were cut at various levels of the cord and medulla and stained by Nissle's haematoxylin and eosin method. Such sections showed considerable congestion of both the anterior and posterior horns, and in some cases numerous capillary haemorrhages both into the adventitial sheath and around the nerve cells, accompanied by an excess of mononuclear cells, with some perivascular infiltration. Distinct neurophagia may be present. On the whole, the nerve cells appear healthy and undistorted, though the borders of some were ill-defined and others stained imperfectly.

Notwithstanding the absence of demonstrable anatomical lesions, definite conclusions may be drawn as to the site and nature of the pathological changes caused by the causal toxin. Judging from the absence of lesions at autopsy and the character of the symptoms in tick paralysis, the action of the toxin seems to be largely confined to the nervous system, the motor function being probably most impaired for, as we have seen, paresis occurs whilst sensation is undiminished, the patient continuing to appreciate stimuli even in the final stages of disease, though making but the feeblest motor response to them.

The apparent integrity of the afferent sensory paths, accompanied as it is by abolition or modification of the reflexes, indicates that the toxin acts upon the central nervous system, *i.e.* upon the motor neurones in the anterior horn, while the undisturbed consciousness or mentality indicate that the cortex is not seriously affected. To determine whether the toxin acts peripherally, the following experiment was tried: (1) A normal dog, which served as control, was anaesthetised, certain spinal nerves (Peroneus communis, Femoral and Median Nerves) were exposed and stimulated with a Faradic current, using a battery fitted with primary and secondary induction coils. The points along the nerve at which separation of the primary from the secondary coils failed to produce any obvious response on stimulation were noted. (2) A dog in an advanced stage of tick paralysis, the animal being unable to stand, was similarly anaesthetised, and the same series of nerves as described under (1) exposed. Stimulation along the nerves of Dog (2) produced a normal and powerful response. This result indicates that the toxin does not act peripherally and, since there is little evidence that the cortex is affected, it would seem as if the motor neurones in the anterior horns and nerve cells of the cranial nerve nuclei are chiefly involved.

The toxin appears to be rapidly absorbed, probably by the blood stream. If absorption took place slowly along the nerves leading from the site of the tick's attachment, it is probable that symptoms would sometimes begin after the removal of the tick, but this has never occurred. Even in the early stages

of the disease there is evidence of the neurones at all levels of the cord being affected, as shown by the dilatation of the pupil, the inability to bark or masticate hard food, and the loss of coordination in the hind limbs.

It may be asked why are not more definite lesions seen in the spinal cord of animals dying of the disease, especially where the course of the disease has been prolonged as in *Case A*. Considering that no permanent, or even prolonged disturbance of function is ever observed in animals recovering from the disease, distinct degeneration or death of the nerve cells can scarcely be expected to occur prior to the animal's death. This is in strong contrast to the degeneration of nerve cells seen in anterior poliomyelitis of man, a disease which frequently results in permanent paralysis of either the whole or part of certain muscles, depending on whether all or part of the neurones responsible for their innervation are destroyed. It is argued therefore that in tick paralysis, though the action of the toxin is sufficient to cause such disturbance of function that the attack frequently ends in death, yet death of the nerve cells does not precede the animal's death, this directly depending on respiratory paralysis. Where the toxin is neutralised or eliminated before this respiratory paralysis is produced, rapid recovery of function follows. Anderson Stuart (1894) states that peripheral nerve paralysis may follow an attack, but it is very doubtful whether the cases he mentions were true cases of tick paralysis and not due to the after effects of a disease like "distemper."

Certain pathological effects due to immature ticks.

Although tick paralysis is due to the adult female tick only, it seems advisable to mention briefly the pathological effects that have been observed to follow infestation with the immature stages of *Ixodes holocyclus* and other tick species. Hadwen and Nuttall (1914) found larvae and nymphs of *Dermacentor venustus* to cause the deaths of the guinea-pigs on which the ticks gorged, though symptoms of paralysis did not occur. In Australia, Cleland (1924) records the case of a colleague who became infested with hundreds of larval ticks which caused intolerable itching, headache, and nausea, so that on the second to fourth days after infestation he was incapable of working; blood smears were negative, and the patient recovered after the sixth day. Paradice (1924) reports that *I. holocyclus* larvae caused urticaria on himself and a colleague, the irritation and papular lesions lasting for a week. I observed similar effects on myself after allowing 25 *I. holocyclus* larvae to attach themselves upon my arm; hyperaemia and itching were caused round the site of each tick bite and lasted for ten days. There is no record of larvae causing serious constitutional symptoms, though Cleland (1912) reports heart symptoms in a man on whom some hundreds of ticks became attached; but it is not stated to what stages these ticks belonged. A certain degree of prostration occurs in men subjected to heavy infestation by larvae, this being probably due to nervous exhaustion caused by the constant irritation; in no case have symptoms of paralysis been seen. *I. holocyclus* nymphs which became en-

gorged on my arm caused similar but severer effects than did the larvae. The immature stages of *I. holocyclus* seem to become engorged by preference on small animals like the bandicoot, rather than on man or domesticated animals, since on small animals taken in autumn or early winter, it is customary to find several hundreds. The immature stages of *Dermacentor venustus*, according to Parker, show a similar preference for different hosts.

III. ETIOLOGY.

Eaton (1913), Hadwen and Nuttall (1914), Todd (1915), Dodd (1921) and Ferguson (1924) suggested two possible hypotheses as to the cause of tick paralysis: (*a*) that the causal agent is a living organism (protozoal, bacterial or filtrable virus) or (*b*) a venom or toxin secreted by the tick.

In support of hypothesis (*a*), Hadwen and Nuttall (1914) note that in the tick paralysis experimentally induced in the dogs by *D. venustus*, no symptoms develop till the tick becomes nearly replete after being six days on the host. The same holds for *I. holocyclus* according to Dodd. There is indeed no positive evidence that paralysis ever occurs until the tick has almost completed engorgement, this having also been observed by me in all of my experimental cases. Such results suggest that the causal agent is a living organism which must undergo a period of incubation in the dog such as is frequently observed in bacterial or protozoal diseases. Moreover, ticks gorging normally on susceptible animals may not produce ill effects, as observed both by Dodd and myself. This might be due to some ticks being non-infective. No further evidence has been brought forward in support of hypothesis (*a*).

Evidence in support of hypothesis (*b*), Hadwen and Nuttall, as a result of their observations on *D. venustus*, incline to the opinion that tick paralysis is caused by a venom or toxin secreted by the tick during engorgement, because they could not find any organism in blood smears or transmit the disease from affected to healthy animals. Similarly Dodd (1921) was unable to demonstrate any organism in the blood or body-fluids of a dog dying of tick paralysis caused by *I. holocyclus*, and Ferguson (1924) failed to find organisms in a fatal case in a child, caused by the same species of tick. Further, the wide range of hosts in which a single species of tick can cause paralysis is suggestive of the causal agent being a venom or toxin. Thus *D. venustus* may cause tick paralysis in either man, dog, cattle or sheep, while *I. holocyclus* causes paralysis in man, dog, cat, sheep, and probably also in the foal, calf and pig.

Personal Observations.

In all my experiments it has been impossible to discover any causal organism in the blood or body fluids, or to transmit the disease to other dogs or experimental animals by the subcutaneous, intravenous or intraperitoneal inoculation of blood, cerebro-spinal fluid, or emulsions of nerve tissues, while the injection of intestinal contents of ticks which had caused fatal attacks also had no effect. Furthermore, observations on the tick in relation to the time

when the symptoms develop lend support to the view that we are not dealing with an incubative period like that which occurs in infective diseases, for the onset of symptoms depends directly upon the stage of engorgement attained by the tick, and, as we have seen, the rate of engorgement may vary considerably. Thus, when ticks engorge slowly, as in *Cases B* and *C* (p. 414) symptoms were not observed for 13 and 12 days respectively, whereas in those cases where ticks engorge rapidly symptoms are most frequently seen 5 or 6 days after the attachment of the tick. It has also been repeatedly observed that when ticks are removed before any symptoms develop, even when the ticks are left in position until almost completely gorged, an attack has never developed. Were the causal agent a living organism, we should expect that when ticks were left on dogs until they had reached a stage at which paralysis commonly occurs, in some cases at least, an attack would develop after their removal.

The following experiments with *I. holocyclus* show that the host on which the immature stages gorge has no influence upon whether such a tick proves pathogenic or not as an adult female. In addition they lend support to the venom theory of the causation of tick paralysis.

Dog 9. (*a*) An adult tick, which emerged from a gorged nymph taken from Bandicoot 4, engorged fully in 8 days upon the dog but produced no symptoms. (*b*) A second adult tick which emerged from a nymph taken at the same time and from the same Bandicoot as the last, engorged fully in 7 days, but produced no symptoms. (*c*) An adult tick collected as a gorged larva from Bandicoot 4, and gorging on it also as a nymph, engorged on the dog and in 6 days produced fatal paralysis. A period of 6 weeks elapsed between the time of engorgement of the second and third ticks.

This shows that the animal on which the nymph engorges does not render the tick pathogenic.

Dog 13. (*a*) Four adult ticks emerged from nymphs that had gorged on a dog, but as larvae had gorged on Bandicoot 5, engorged on dog in 7–11 days without producing any ill effects. (*b*) One tick collected from the same Bandicoot as a larva, and engorging on it also as a nymph, when semi-gorged on the dog produced a mild attack of paralysis, from which the dog recovered after the removal of the tick.

Dog 14. (*a*) Two ticks which engorged as larvae and nymphs on Bandicoot 5, engorged fully on dog in 7 days, producing no ill effects. (*b*) Two ticks which had gorged as larvae on Bandicoot 5, produced fatal paralysis in a dog in 6 days.

The foregoing experiments show that the hosts of the immature stages bear no relationship to the pathogenicity of the adult female tick.

Efforts were also made to determine whether the hosts on which the parent tick gorged influenced the pathogenicity of the progeny. For this purpose a second generation had to be reared in captivity, the host being the same at all stages. This was accomplished but it was only possible to obtain 9 females in the second generation. Of these 8 gorged on Dog 19 but without producing any ill effects. No conclusions can therefore be drawn as to this final hypothesis.

IV. THE SALIVARY GLANDS OF TICKS.

From the facts elicited, both in Australia and elsewhere, the close relationship of the stage of engorgement of the tick to the onset of an attack of tick paralysis is clearly defined. It would appear, therefore, that some change in the physiological activity of certain organs of the tick during the final rapid stage of engorgement is responsible for the production of the toxic agent.

Dissection of numerous ticks which had engorged for 4 and 5 days revealed in all cases enormous development of the salivary glands compared with the size of these in ticks which had been engorging for from 2–3 days. These glands from their great development, and having their salivary ducts running forward to open into the base of the buccal capsule in close proximity to the tissues of the host, suggest themselves as a very likely source of the toxin.

The histology of the salivary glands in ticks has been studied by Nordenskiöld (1909), Bonnet (1906), Samson (1909) and Robinson (1914).

Robinson dealt with the salivary glands of *Argas persicus*, while the other authors described those of *Ixodes ricinus*. In both of these species two types of alveoli were found, the greater part of the gland being made up of (*a*) large pear-shaped alveoli, arranged in grape-like clusters on branched efferent ducts, (*b*) fewer and much smaller rounded alveoli, each of which opened by a short unbranched duct into the main salivary duct. In *Argas* these smaller alveoli were aggregated together in the anterior half of the salivary gland or the mesial side of the main salivary duct, while in *Ixodes*, instead of being aggregated into a compact mass, they are scattered along the course of the larger salivary ducts into which they open directly by short unbranched ducts.

Salivary glands of Ixodes holocyclus: Dissections were made as advised by Robinson (1914) except for the tick being in a fresh state (no coagulation by boiling water); normal salt solution was constantly used to wash away the intestinal contents which obscured the dissection.

The appearance of the glands varies considerably according to the stage of engorgement of the tick. In the later stages the glands appear as prominent pearly white masses occupying the greater part of the anterior half of the body cavity. In partially gorged ticks the glands are much less conspicuous, the alveoli being very much smaller (see Figs. 1, 2).

A superficial examination may lead one to suppose that the gland is wholly composed of (*a*) large pear-shaped alveoli, but on removal and mounting, (*b*) a second type of alveolus is revealed. These are much smaller than (*a*) and are limited in their distribution to the main salivary duct; they do not extend along even the larger branches, while each alveolus opens into the main duct by a short efferent duct. There is no doubt that these alveoli correspond to the second type of alveolus described by Bonnet and by Samson in *Ixodes ricinus*, though the latter states in that species they are distributed along the larger branches of the salivary duct throughout the gland.

Sections of the glands stained with acid haematoxylin and counterstained with eosin, or with thionin and orange G, showed marked variation in the staining properties of the cells of the two alveoli. Thus, while the first type of alveoli (*a*), during development, show great affinity for basic stains, the second type (*b*) appear as but pale ghosts surrounding the main salivary duct, their nuclei alone standing out sharply amidst their delicate fibrillar structure.

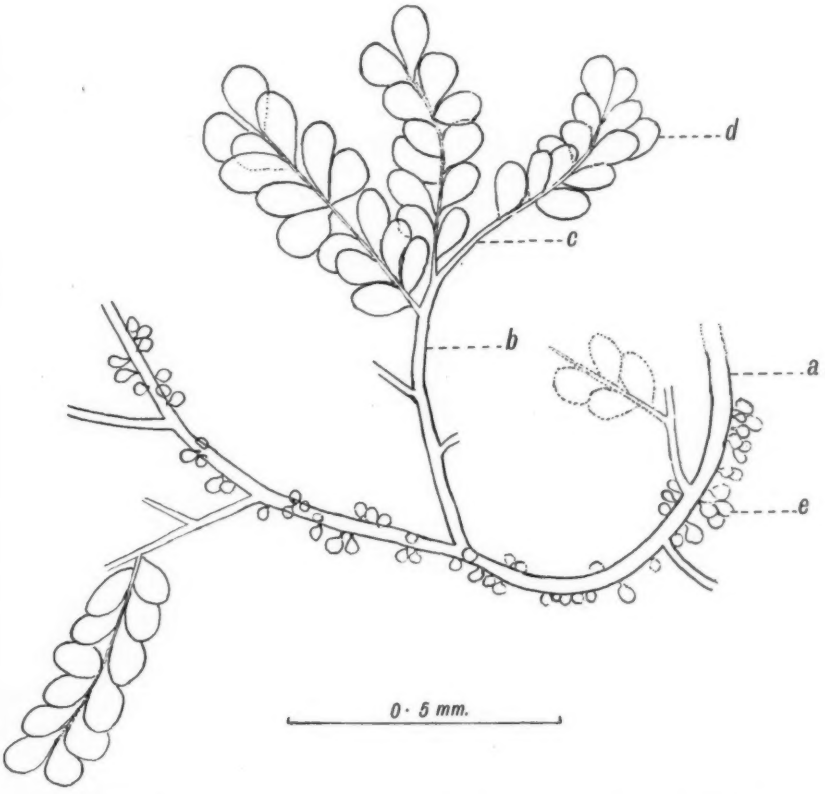

Fig. 1. Showing the general appearance of a part of the salivary glands of one side and the arrangement of the two types (large and small) of alveoli. Drawn to scale, unstained.

Nordenskiöld (1908) discusses the possible function of the two types of alveoli. Bonnet (1906) considered the second type of alveoli resembled the venom cells of snakes.

It was not possible to determine the function of each of the two types of alveoli in *Ixodes holocyclus*. It may be mentioned that a similar character and distribution of alveoli was found in the salivary glands of *Haemaphysalis*

bispinosa, Boophilus australis, Rhipicephalus sanguineus, and *Amblyomma* sp. from the Blue Tongue Lizard (*Piligua stincoides*).

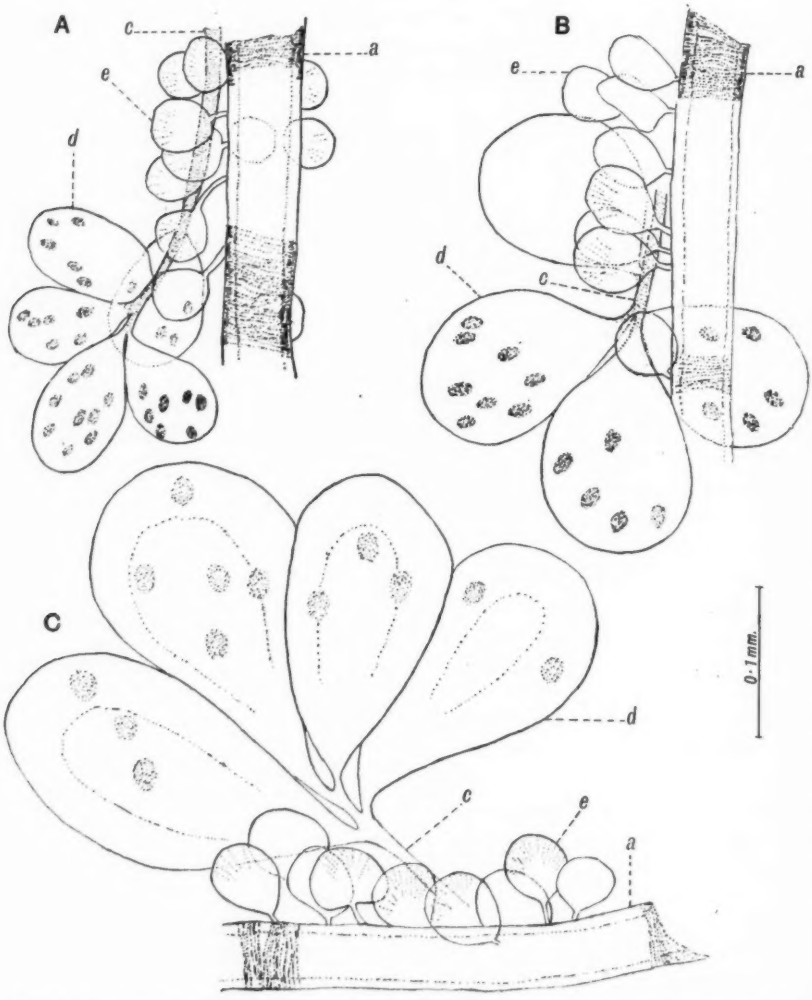

Fig. 2. Showing the relative size of the alveoli of the salivary glands in ticks that have fed for (*A*) 2 days, (*B*) 3 days, and (*C*) 5–6 days. All drawn to the same scale, unstained.

a = main salivary duct (only partly shaded), *b* and *c* = secondary and lobular ducts, *d* and *e* alveoli of the first and second types (large and small) respectively.

Dissections of the salivary glands of gorged nymphs and larvae of *I. holocyclus* show them to have the same structure as in the adult.

V. THE SALIVARY SECRETION OF TICKS.

Sabbatani (1898), in a paper quoted at length by Nuttall and Strickland (1908), found that the bodies of *Ixodes ricinus* contained a substance which retarded the coagulation of human and dog's blood. If large doses of an emulsion of chopped up ticks (1 gramme per kilo body-weight) were injected intravenously into a dog, in addition to inhibiting coagulation of the blood for 24 hours, grave symptoms were shown by the dog during the course of the injection. These were characterised by a fall in blood pressure and rapid heart beat, while respiration was slowed and then ceased. In those cases where animals did not die there was marked prostration, loss of reflexes and even complete paralysis. Smaller doses of the tick extract injected into dogs and cats caused vomition, diarrhoea and loss of coordination, but the animals recovered in a few hours.

Nuttall and Strickland (1908) definitely showed that the salivary glands of *Argas persicus* contained an anticoagulin, by dissecting out the glands and emulsifying them with a minimal quantity of sterile saline. When equal quantities of this emulsion and blood were mixed, clotting was either delayed for varying periods or completely prevented. They showed also that the amount of anticoagulin contained in the salivary glands of individual ticks varied very considerably. The authors sought to reproduce the results obtained by Sabbatani, using emulsified salivary glands of *Argas persicus* (instead of *I. ricinus*), but when these were injected subcutaneously into mice, fowls and rabbits, the results were negative.

Todd (1914) found that the intestinal contents of *Dermacentor venustus* also contained anticoagulin.

Personal Observations.

Using a technique similar to that of Nuttall and Strickland, I found that emulsions of salivary gland taken from partially gorged ticks, when mixed with equal or double quantities of blood, prevented coagulation for more than 2 hours, showing that the salivary glands of this species also contain anticoagulin. There was no evidence of the presence of a haemolysin however. The salivary secretion tested with Phenophthalein and Congo Red appeared to be almost neutral and at most only faintly acid in reaction.

It remained then to show whether the presence of a definite toxin could be demonstrated in the salivary glands, sufficient at least to implicate them as the source of the toxic agent of tick paralysis. Sabbatani's findings in regard to *I. ricinus* are very suggestive in view of the recent association of this species with paralysis of sheep in Crete.

(I.) One female, after engorging on a dog till the 5th day, was removed and the salivary glands dissected out with aseptic precautions. These were then emulsified in 0·75 c.c. normal saline and injected subcutaneously into a white mouse. A control mouse received an equal dose of sterile saline. Mouse 1 was kept under observation for 2 hours, during which time it showed little inclination to move and its gait appeared stiff and difficult. The

following morning it was found dead. No lesions were discovered at autopsy. The control mouse remained bright and normal.

(II.) Salivary glands from a completely engorged female were dissected and emulsified in sterile saline and injected subcutaneously into a guinea-pig. Result negative.

(III.) Salivary glands from two ticks which had produced an attack of paralysis which terminated fatally in Dog 14 were injected subcutaneously in 5 c.c. of sterile saline into a small dog. Result negative.

(IV.) Two ticks which produced a fatal attack of tick paralysis were removed, while partially gorged, from the affected dog, their total weight being 200 mgm. They were placed in 70 per cent. alcohol for 5 minutes, washed in repeated changes of sterile saline and then dissected with aseptic precautions. The salivary glands and intestinal contents were then emulsified with saline and strained to remove any large particles of solid matter. The emulsion, in 3 c.c. of normal saline, was then injected into the jugular vein of a fox terrier weighing 4·5 kilos. Prior to the injection the dog's temperature was 102·6° F. Forty-five minutes later the dog's temperature was 103·3°, the animal was dull, depressed and refused to run about in its usual lively way. One and a half hours after, the animal appeared somewhat less depressed and ate some of its evening meal. The following morning it was bright and lively and showed no further effects.

(V.) Four ticks were removed from a dog which subsequently died of tick paralysis, all being only partially gorged and weighing altogether 175 mgm. They were placed in 70 per cent. alcohol for 5 minutes and then before dissection washed in repeated changes of sterile normal saline. They were then dissected with aseptic precautions and the salivary glands only were removed as cleanly as possible. The glands were emulsified in 3 c.c. of saline and, after straining through sterile muslin, were injected intravenously into a dog weighing a little under 5 kilos.

The injection was made at 10.30 a.m., the dog's temperature being 102° F. One hour later the dog was seen to have vomited its morning meal; it was quiet and refused to run about when taken out of its box. At 12 midday the temperature was 105·2° F. The dog on being made to move appeared very depressed, with tail drooping, the eyes dull and the expression dejected and stupid. On being made to walk some distance, the animal moved unsteadily and the hind quarters swayed slightly but distinctly.

At 2 p.m. the temperature was 103·2° F., and the dog was still dull and little inclined to move. At 5 p.m. the animal appeared much brighter and was ready to run about and ate most of its evening meal, the temperature at this time being 102° F. The following day the dog again appeared bright and it showed no further effects.

The foregoing experiments only yielded appreciable results in two instances: I and V. The death of Mouse No. 1 may have been due to a toxin, but reliance cannot be placed on a single experiment.

In Experiment V, the dog showed certain definite effects very shortly after the injection, though these were transitory. Were the effects due to an injected toxin or merely attributable to a foreign protein thrown into the circulation? It is noteworthy that in Experiment V, the dog's symptoms were relatively severe though it received less protein than the dog in Experiment IV, the latter having been injected with salivary gland emulsion and the gut contents of 2 ticks which together weighed more than the 4 from which only the salivary glands were taken for the injection in Experiment V. This might indicate that the foreign protein is not the active substance but that it is to be found in the salivary glands.

If the salivary gland secretion induces tick paralysis, why are more definite symptoms not produced by the injection of salivary gland emulsion? This may be explained by the circumstance that when the tick feeds, especially during the final stage of engorgement, much more salivary secretion must be emitted by the glands than can be present at any one time in the glands themselves.

In Sabbatani's experiments, previously cited (p. 423), the severest effects followed when the largest doses of tick emulsion, equal to 1 gm. of tick per kilo of dog were injected. Moderate doses had less effect whilst small doses exerted little or no effect. My Experiment IV was similar to those of Sabbatani except that only 0·05 gm. per kilo was injected into the dog. Of this dose but a very small part would represent the salivary glands and these would have to contain an exceedingly potent toxin to produce distinct symptoms. Data are at present lacking to permit of a comparison between the toxicity of snake venom and the toxin present in certain ticks; it would seem to be a subject worthy of investigation.

Progressive activity of the tick's salivary glands during engorgement. There is an enormous increase in the activity of the salivary glands corresponding to the final rapid phase of engorgement, *i.e.* the period when there is a greatly augmented intake of blood which reaches its maximum during the last 24 hours before the tick abandons its host. Dissections of ticks at varying stages of engorgement illustrate this very strikingly (see Fig. 2, p. 422). After 24 hours' feeding, the salivary glands are small and inconspicuous, the alveoli, especially those of type (*a*) (see p. 420), are small and undeveloped. Even after 48 hours, when the glands are more readily isolated, the alveoli are still small. After 4 days, however, they have become greatly enlarged and some, having attained the maximum size, are distended with secretion or discharging their secretion into the alveolar lumen, this being seen in microscopic sections. On the 5th and 6th days, in ticks that have fully gorged in 6 days, the alveoli are found uniformly large but for those which have discharged their contents and collapsed. The progressive increase in the weight of a gorging tick affords an indication of the relative amount of salivary secretion that is given off at different times. The unfed female tick weighs *ca.* 1 mg.; on the 4th day it may weigh only 20 mg., but on the 6th day a moderately replete tick may weigh 450 mg. Therefore the tick's weight has increased over twenty-fold in the concluding 4 days, and doubtless the production of salivary secretion increases correspondingly. This appears to explain why symptoms in the dog usually commence on the 5th day after the tick has become attached, for it is only then that the dog is the recipient of enough toxin to exert a material effect. It seems probable that the properties of the secretions emanating from the two types of alveoli (*a*) and (*b*) differ.

VI. IMMUNITY.

Natural immunity. There is a popular belief that certain dogs are naturally immune but the evidence is untrustworthy. Dogs regarded as immune have often succumbed to tick paralysis. The belief may depend upon immature ticks having been often found on dogs, it not being recognised that only the female tick causes the disease. Moreover, it is not every female that is capable of producing tick paralysis. Several females may gorge on a dog and produce no ill effects without the dog being immune; a single tick may cause a fatal attack in the same dog subsequently. Nevertheless there seems to be definite evidence that certain dogs living in tick-infested places for many years, whilst constantly exposed to infestation, never suffer ill effects. No positive evidence of immunity was obtainable from any of my experimental cases.

The severity of the attack and rapidity with which death occurs, may in a measure depend upon the age and size of the dog. It was found with experimental cases that small dogs died more quickly than did large ones. In the case of a dog weighing 20 kilos and aged 3–4 years, fatal paralysis could not be produced. A dog aged 6–7 years succumbed to tick paralysis naturally acquired, therefore age is not necessarily a safeguard. The relative resistance of large dogs, as compared to small ones, may well depend upon the dose of tick-derived toxin being smaller in proportion to its body weight.

Acquired Immunity. Two attempts were made to see if dogs acquired immunity after recovering from an attack of tick paralysis:

Experiment I. Dog 5. (*a*) One tick induced an attack from which the dog recovered after the tick's removal. Four days after the animal again appeared normal and (*b*) 8 days after the first tick's removal, a second tick was placed on the dog. This tick caused a fatal attack, death occurring after 5 days.

It may be argued that in this case immunity could not become established in the short time that was allowed to elapse after the first attack.

Experiment II. Dog 13. (*a*) One tick produced a mild attack in this dog—there was distinct incoordination and general motor disturbance and the dog could not bark. (*b*) *Five weeks* after the first tick was removed, 3 ticks were placed on the dog; two of the ticks became engorged whilst the third died. The dog showed no ill effects. (*c*) *Two months* later the dog was allowed to run in tick-infested country and acquired 5–6 female ticks which were thought to have become fully gorged. On the 8th day when the last tick dropped off, the dog showed symptoms (slight incoordination, difficulty in rising, inclination to fall when running) but recovered. (*d*) *Two weeks* after recovery, 5 ticks became attached and gorged fully upon the dog without ill effects. (*e*) *Three weeks* and (*f*) *five weeks* later 7 and 4 ticks respectively gorged upon the dog without effect. The dog was then returned to the University of Sydney where (*g*) 10 laboratory-reared ticks were allowed to attach themselves to the animal (three died on days 1 and 4, three were removed on days 2, 3, and 4 respectively); the remaining four ticks gorged normally in 5–6 days. Apart from local irritation no effect resulted.

Therefore, after recovering from two mild attacks of paralysis, 20 ticks gorged upon the dog without effect on four occasions. This experiment shows

that the first mild attack did not confer a sound immunity, it may well have been partial because the second attack was mild.

Whilst very suggestive, the foregoing experiment does not permit of final conclusions being drawn regarding acquired immunity. Such experiments should be repeated and varied.

SUMMARY.

1. Tick paralysis occurs in man, the dog, and other domesticated animals on the East Coast of Australia.

2. As far as is known, the disease in Australia is only conveyed by the mature female of *Ixodes holocyclus*. The immature stages and the male of this species of ticks are non-pathogenic.

3. A similar disease, induced in a like manner by females of other species of ticks, has been observed by various authors in South Africa, Canada and Crete.

4. A single tick, as shown by experiment, may cause fatal paralysis in the dog in Australia, the death-rate in dogs being very high.

5. The main symptoms of tick paralysis in Australia do not differ materially from those observed in other countries. They begin with loss of coordination commencing in the hind legs in dogs, the fore legs, head and neck becoming subsequently affected. Death in all cases appears to be due to respiratory paralysis.

6. The onset of symptoms has not been observed to occur in less than 5 days from the time the tick or ticks have attached themselves to a dog.

7. Some of the ticks do not produce paralysis and others do, as shown repeatedly from my experiments on dogs. This requires explanation. It does not depend on the time that has elapsed between the tick having moulted and its attacking the dog.

8. Paralysis has never been seen to occur when ticks were removed from dogs before the time when symptoms usually appear.

9. It is impossible to transmit the disease from affected to healthy animals by the inoculation of blood, cerebro-spinal fluid or nervous tissue. Nor can the disease be transmitted by the injection of the body contents of ticks removed from affected animals. The examination of the fluids and organs of affected animals has failed to reveal the presence of pathogenic organisms.

10. It is considered that the causal factor in the production of the disease is a tick-derived toxin, this toxin being secreted by the salivary glands.

11. During the process of engorgement the salivary glands develop greatly, pouring out a maximum amount of secretion during the 2 days before the female tick drops.

12. An emulsion of salivary glands of *I. holocyclus* proved to be toxic for when injected into a dog (Experiment V, p. 424) it caused fever, vomiting, etc. The salivary secretion contains anticoagulins. As Nuttall and Strickland found for anticoagulins, individual ticks may vary in toxicity.

13. The period which elapses between the attachment of a tick to the host and the first signs of an attack of tick paralysis cannot be regarded in the light of an incubation period; it is dependent on the rate and stage of the tick's engorgement.

14. If it be accepted that the causal agent of the disease is a tick-derived toxin, it remains to be shown how such a toxin is produced.

15. There is some evidence that immunity to the disease may be acquired after recovering from previous attacks.

16. There is no evidence of season having an influence on tick paralysis. It was induced experimentally both in winter (June–August) and summer (November–December) in Sydney.

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THE OCCURRENCE OF *CUTEREBRA* (DIPTERA, OESTRIDAE) IN WESTERN CANADA.

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(With 1 Figure.)

Reference to the National Insect Collection at Ottawa shows that species of the genus *Cuterebra* have been collected in various localities of Western Canada at different times. Of these *Cuterebra grisea* Coq. is distributed throughout Manitoba, Saskatchewan, Alberta, North-West Territories and British Columbia. There is one record each of *C. emasculator* Fitch (determined by Aldrich as *C. fontinella* Clark), of which the locality is unknown, and of *C. fasciata* Swenk, from Peachland, British Columbia. The specimen of *C. emasculator* bears a note that it had been reared from a chipmunk, *Tamias striatus lysteri* Richardson. The remaining species, *C. americana* var. *polita* Coq., *C. similis* Johnson and *C. tenebrosa* Coq. have all been collected in British Columbia. There is but a single record from the Eastern Provinces and that a specimen of *C. fasciata* from Bathurst, New Brunswick, dated August, 1900. Altogether there are 22 specimens in the National Collection belonging to six species. Of these there are 11 specimens of *C. grisea*, which would thus appear to be the most prevalent species in Western Canada. The comparative paucity of specimens may be correctly attributed to the peculiarly shy habits of the species, the adults of which, according to information furnished me by Criddle, prefer rather dark situations, such as outbuildings, summer kitchens and the ground burrows of rodents. They occur on the wing from June to September and are probably to be found closely attendant upon the haunts of their rodent hosts. That the percentage of parasitism is not high is concluded from the fact that Parker and Wells (1919), in a careful examination of over a thousand rodents in Montana for possible infestation by the Rocky Mountain spotted fever tick, *Dermacentor venustus* Banks, found but two that were parasitised, each with one larva of *C. tenebrosa*.

Apparently very little is known concerning the hosts of *Cuterebra* in Western Canada, and what information we have is due to the efforts of Criddle, at Aweme in Manitoba, and Hadwen (1915), now of the University of Saskatchewan and previously Animal Pathologist in British Columbia. Mr Criddle informs me that he has reared adults of *Cuterebra* from a gopher, a vole and a rat, one specimen in each case. In the case of the rat 17 larvae were found, and whereas the presence of one or two larvae does not appear to

inconvenience the host, Criddle noted that this particular rat was in a decidedly emaciated condition. Added to these records there is one of the discovery of three larvae in a house mouse at Aweme in 1921. An unpublished record by Hadwen has reference to the finding of a larva in a house mouse at Agassiz in British Columbia in September, 1916. This larva pupated; the adult emerged on May 14, 1917, and remained alive for two weeks. This specimen was determined as *C. grisea* by Townsend.

Although small rodents seem to be the natural hosts of cuterebrid larvae in Canada, their presence in cats and dogs is not unknown. Hadwen (1915) records the discovery by a correspondent of two mature larvae, which were extracted from the costal region of a domestic cat in Manitoba. Another interesting record has kindly been furnished me by the same author, to whose attention it was brought in 1918. This concerns the infestation of a dog at Côteau du Lac, near Montreal. The animal was treated for sickness by a veterinary surgeon, A. A. Etienne of Montreal, who discovered two cuterebrid larvae beneath its skin. In the process of extraction the smaller one of the two larvae was accidently crushed and its body left beneath the skin of the host. As a result the dog developed symptoms of pronounced anaphylactic shock, including frothing at the mouth, vomiting and running at the eyes. Respiration became accelerated and was accompanied by diarrhoea. The animal seemed blind and had incoordination and vertigo. The symptoms persisted for several hours, but eventually the animal recovered completely. From this same dog 13 additional larvae were subsequently removed in the interval from September to December, 1918. It was noted that the larvae appeared in those parts of the host where the skin was thin, particularly in the region of the scapulo-humeral articulation. The owner of the dog had observed, previous to the appearance of the larvae, that it had been attacked by an insect, which was described as resembling a bee and was probably a *Cuterebra*. This observation suggests that infestation of the canine host may be direct, *i.e.* that the female insect deposits its eggs on the host, although it is not unlikely that carnivores may occasionally become infested indirectly by eating the carcases of rodents containing immature larvae, which migrate from the stomach to the skin in the new host, and there complete their development. This contingency has been suggested by Hadwen (1915) and also by Aldrich in a paper by Crawley (1923), who cites a case, reported by French, of a cuterebrid larva (*C. emasculator*) found in a dog's scrotum at Montreal. In the United States, Hall (1925) has records of 16 cases of the occurrence of cuterebrid larvae in cats, and Crawley records a single larva from a dog in Pennsylvania.

In July, 1918, a correspondent at Dalesboro, in south-eastern Saskatchewan, sent to the University of Saskatchewan four out of five cuterebrid larvae which he found beneath the skin of a brown rat, *Rattus norvegicus* Erxleben. The host was killed in a hayfield about a mile distant from the nearest farm buildings. One of the larvae occurred on the back, two on the posterior region

of the abdomen and the remaining two on the anterior region of the body near the fore-legs. This constitutes the first record of cuterebrid parasitism of the rat in Saskatchewan. Since its first reported occurrence (1925) at Gainsboro in the extreme south-east corner of Saskatchewan in 1912, the Norwegian rat has gradually spread in a westerly and northerly direction until it has now become established over an area of about 16,000 square miles, including all the territory, which extends east of a line drawn from the international boundary through Lampman, Broadview, Springside and Preeceville. Its line of advance is yearly becoming more extended, and it will be interesting to watch what the relationship of *Cuterebra* to its increase may be.

Description of Larvae.

The larvae from Dalesboro were almost full-grown, coriaceous, of a brownish black colour and averaged 15·5 mm. long and 7·6 mm. broad. In addition to the small head segment there are three thoracic and eight abdominal. Compared with a larva taken from the back of a mouse at Richland, Manitoba, on September 5, 1918, and referred to me by the late Dr C. Gordon Hewitt, this specimen was slightly larger, measuring 17·5 mm. long and 10 mm. broad. The latter, however, had been compressed dorso-ventrally probably in the process of removal from its host. In other respects it agrees closely with the rat larvae from Dalesboro, only its colour is a jet shiny black with the spinous armature more closely set, so that no cuticular interspaces between the individual spines are apparent. The hollow, flattened, retrorse, spangle-like spines (Fig. 1 C) are in both cases alike, and they resemble each other in that the spines on the anterior halves of the individual body segments have their posterior margins serrate, the remainder being bluntly conical or gently rounded posteriorly, except that a few less pronouncedly serrated spines occur at the posterior margin of each segment save the eighth abdominal. This last segment, bearing the paired posterior spiracles (Fig. 1 B), is fleshy white and slightly rugose, with a few dispersed, relatively small, broad, conical, denticle-like spines, whose pointed ends project forwards. They are numerous on the dorsal and lateral surfaces of the segment, and absent ventrally. The brown, semi-circular, stigmatic areas occupy much more than half of the truncated, posterior surface of the segment and are closely approximated in the median line, where their mesial, straight, peritremal margins (*PT*) face each other. Each stigmatic area bears three markedly sinuous slits (*SS*), each of which spreads out towards the lateral curved peritremal margin. All three gradually become narrowed as they converge to the lower inner angle of the stigmatic area, which they almost completely occupy.

The head segment is fleshy white, rugose, bearing two prominent, bulbous, antennal protuberances separated from each other by a median longitudinal furrow. Each protuberance bears in addition to the minute, two-segmented antenna, a reduced maxillary palp, lying ventral and lateral to the antenna, its depressed apex delimited by a slightly elevated brownish rim. The paired,

downwardly projecting, shiny black, mandibular sclerites (Fig. 1 A, *M*) are exposed ventrally and each tapers slightly to a blunt point. The paired dentate sclerites (*DS*) articulate with the bases of the mandibular sclerites. They are quadri-tuberculate with dorso-median, latero-dorsal, latero-median

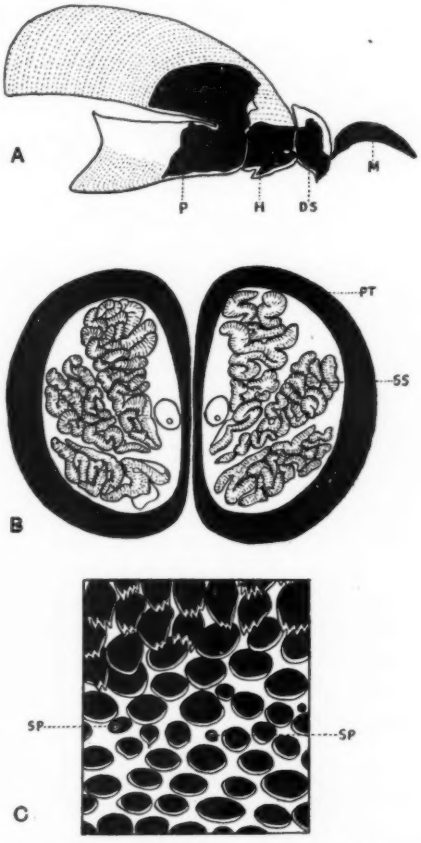

Fig. 1. *Cuterebra* sp. larva from rat. (A) Cephalopharyngeal skeleton, lateral aspect, × 22; *M*, mandibular sclerite; *DS*, dentate sclerite; *H*, hypostomal sclerite; *P*, pharyngeal sclerite. (B) Posterior spiracles, × 50; *PT*, peritreme; *SS*, stigmatic slit. (C) Portion of cuticular armature of second abdominal segment, dorsal region, × 34; *SP*, sensory pit. (A) and (B) balsam mounts, (C) glycerine mount, all sketched with aid of camera lucida.

and ventral pointed projections. The H-shaped hypostomal sclerite (*H*) articulates with the paired, dentate sclerites anteriorly and with the pharyngeal sclerite (*P*) posteriorly. The anterior parts of its lateral limbs are divergent; posteriorly they are convergent. An accessory sclerite of minute size is situated dorsally in the interval between the paired, dentate sclerites. The

stirrup-shaped pharyngeal sclerite is densely chitinised anteriorly. The membranous portion of the lateral lamella is marked with delicate, concentric striae, especially the upper limb, the anterior part of which extends forward and is connected with the dentate sclerite.

At irregular intervals among the spines of the posterior halves of the body segments there occur less densely chitinised, conical elevations, at the apices of which there are present sometimes a single and often two sensory pits (Fig. 1 C, *SP*).

Immediately beneath the chitinous cuticle there is a profusely branching system of minute tracheae, which terminates in twigs of exquisite delicacy in the cavities of the spines as well as in the intervals between the spines. This arrangement would suggest a respiratory function for the latter in addition to the locomotor, and it is not improbable that this integumentary, respiratory mechanism is adapted to the parasitic habits of the larva, whereby gaseous interchange is secured as between the host tissues and the parasite.

The main tracheal trunks terminate anteriorly in the interval between the prothoracic and mesothoracic segments laterally, and the opening of each to the exterior is blocked by a brown, bottle-shaped plug, consisting of a dense mass of stout, elongated, club-shaped hairs.

It is not improbable that the larva obtained from the mouse at Richland, in Manitoba, and those from the rat at Dalesboro, in Saskatchewan, are of one species, differing only in size, that from the mouse being the more mature. It is not unlikely that the species is *C. grisea*, whose habitual hosts in Saskatchewan are probably *Citellus richardsonii* Sabine, *C. tridecimlineatus* Mitchell and various species of field mice. In the National Collection at Ottawa there are two specimens of *C. grisea* from Saskatchewan, one of which was captured at Borden on the North Saskatchewan river, 30 miles north-west of Saskatoon, in August, 1906, and the other at St Louis, about 80 miles north-east of Saskatoon, on July 11, 1898. Moreover, our University collection contains a specimen captured at Goose Lake, 40 miles south-west of Saskatoon, on July 20, 1907.

Acknowledgments. In conclusion I would express my gratitude to Mr Norman Criddle, Dominion Entomological Branch, Aweme, Manitoba, and to Dr Seymour Hadwen, University of Saskatchewan, who kindly placed at my disposal information which they possessed concerning *Cuterebra*. I am also indebted to Dr J. M. Aldrich, United States National Museum, Washington, D.C., who confirmed my determination of the Dalesboro larvae as *Cuterebra* sp. and for his help in providing me with references to the literature of this interesting genus. My thanks are also due to Mr Arthur Gibson, Dominion Entomologist, and his assistant, Mr C. H. Curran, for their kindness in furnishing me with a list of the number and localities of the named species of *Cuterebra* in the National Collection.

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ON *CITTOTAENIA DENTICULATA* (RUDOLPHI 1804), WITH NOTES AS TO THE OCCURRENCE OF OTHER HELMINTHIC PARASITES OF RABBITS FOUND IN THE ABERYSTWYTH AREA.

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(With 4 Text-figures.)

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1. NOTES ON THE HELMINTHIC PARASITES FOUND.

The examination of the rabbits of the Aberystwyth area has shown heavy infection with adult cestodes. Of 516 small intestines of rabbits examined 358, or 66 per cent., have harboured adult cestodes. Two species occur—*Cittotaenia pectinata* (Goeze 1782) and *Cittotaenia denticulata* (Rudolphi 1804). Neither appear to have been recorded for the British Isles before. Theobald (1910) refers to reports of the prevalence of tapeworms in rabbits from near Winchester and from Devonshire. The known distribution of *C. denticulata* is Germany and France, and of *C. pectinata*, Germany and France and a variety, *var. americana*, in North America. *C. pectinata* is found in that part of the small intestine nearest the stomach. *C. denticulata* occurs in the lower part of the small intestine. On no occasion have the two species been found in one rabbit.

Although the examination of the rabbits of the area has been done primarily with reference to the adult cestodes, the occurrence of other parasites has been noted. Two larval cestodes have been found to occur—*Cysticercus pisiformis* on the mesentery of the stomach, and *Coenurus serialis* on the subcutaneous tissues, the former being very common. Three nematodes have been recorded, *Graphidium strigosum* in the mucosa of the stomach, *Trichostrongylus retortaeformis* in the small intestine, and *Passalurus ambiguus* in the caecum and appendix, all being of frequent occurrence in adult rabbits. *Trichostrongylus retortaeformis* has been taken from young rabbits, 4–5 weeks old. On six occasions the larval form of *Pentastomum taenioides* has been taken from the small

intestines of rabbits, the greatest number from one individual being 3. From the wetter districts heavy infection of rabbits with liver-fluke (*Fasciola hepatica*) has been reported during the past winter.

The small intestines of 16 hares were examined between November and February for adult cestodes. *Cittotaenia pectinata* was taken from 3. Two individuals of *C. pectinata* were taken from a hare on January 11th. (Compare Riehm (1881), who states that *C. pectinata* occurs in European hares only in the fall and the first half of the winter.)

2. THE ANATOMY AND HISTOLOGY OF *CITTOTAENIA DENTICULATA*.

(*a*) THE GENUS *CITTOTAENIA*. The genus *Cittotaenia* was proposed by Riehm in 1881 with *Cittotaenia latissima* as type and only species. Later in the same year Riehm discarded the genus and placed the single species in *Dipylidium*. In 1891 Blanchard proposed the genus *Moneizia*, based on the number of genital pores, and included in it the double-pored cestodes of ruminants and rodents. Stiles in 1893 excluded the cestodes of rodents from the genus *Moneizia* without classifying them. In the same year Raillet proposed the genus *Ctenotaenia* with *Ctenotaenia marmotae* (Frolich 1802) as type species. The priority of *Cittotaenia* over *Ctenotaenia* was pointed out by Stiles in 1896.

Stiles (1896) subdivided the genus into two groups: (1) the Marmotae or Denticulata group in which the cirrus pouch is pyriform, distinct and very muscular, and (2) the Pectinata group in which the cirrus pouch is more elongated, resembling the nozzle of a hose, and less distinct. Hall (1908) added the character of the cirrus pouch being "swollen proximally by a vesicula seminalis" to the diagnosis of the Marmotae group. Douthitt (1915) added the following diagnostic characters:

Marmotae group—dorsal duct lateral or dorsal of ventral;

Pectinata group—dorsal duct median to the ventral.

Cittotaenia is the only genus of rabbit cestodes represented in both the Old and the New World.

The type species of the genus, *Cittotaenia denticulata* (Rudolphi 1804), belongs to the Marmotae group. It has been found to be of frequent occurrence in the rabbits of the Aberystwyth area. An account of the history and synonymy of this species is given by Stiles (1896). The fullest description has been that of Riehm (1881) from Saxony, but his account of the anatomy is inadequate and no histology is given. A study of the Aberystwyth material has shown several points of difference from Riehm's account. They will be referred to in detail after the writer's description of the anatomy and histology of the Aberystwyth material.

Differences of lesser magnitude and importance and agreements between the descriptions of Riehm and the writer are indicated in the text.

No anatomical work has been done on the species since Stiles's account in 1896. The references to it after that date are as follows: Du Buysson (1904),

notes its occurrence in a rabbit in France; Bourquin (1905) compares the strobila of *Bertia elongata* with that of *C. denticulata*; Janicki (1906), in an account of *Triplotaenia mirabilis*, refers to the long horns of the pyriform body of *C. denticulata*; Ransom (1909) refers to the species as the type of the genus; Theobald (1910) includes *C. denticulata* in a list of rabbit cestodes; Galli-Valerio (1910), referring to the species by its synonym *Ctenotaenia goezei* (Baird 1853), records its occurrence in Garrene, France; Douthitt (1915) refers to it as the type species of the genus; Underhill (1920) gives the following description of the species: "the head is small with flat suckers. The neck is as broad as the head. The larger segments may be 10 mm. in width, always wider than long. The genital pores are on the posterior fourth of the border of the segment. It may reach a length of 8 cms." No indication as to the basis of this description is given. The species does not occur in America (Stiles 1896). The head of the species is comparatively large, there is no neck, the larger segments may be up to 15 mm. in width, and individuals 70 cms. long have been taken; Stiles (1896) gave the known distribution of the species as Germany and France. The writer has been unable to find any subsequent statement as to its occurrence elsewhere.

(*b*) Technique. The material for both sections and whole mounts, on which the following description is based, was fixed in a corrosive sublimate solution consisting of one part of saturated corrosive sublimate solution, one part of 70 per cent. alcohol and a few drops of glacial acetic acid. The fixative was washed out with iodine-alcohol and water. Transverse, longitudinal, and facial serial sections were cut and stained in Mann's stain. Satisfactory transparency mounts were difficult to make owing to the thickness of the segments. Those prepared were stained either with Ehrlich's acid haematoxylin or with borax-carmine.

(*c*) General Appearance. The strobila when fresh has a deep yellowish tinge. Riehm describes its colour as "grey, or reddish grey, like *Dibothriocephalus latus*." The thickness of the segments gives the worm a fleshy appearance, most marked in the gravid segments. The prominent genital papillae near the posterior corners of the segments, and the readily discerned cirri which are protruded from them in the mature portion of the strobila, are distinguishing features of the species. In mature individuals the cirri are protruded first at about the 110th segment (compare Stiles (1896) who gives the 78th segment). The cirri and the suckers are pigmented black as described by Riehm. The overlapping of the segments is very marked and constant. The young has a narrow rod-like form with the scolex as a prominent knob at the anterior end.

(*d*) Scolex. The general appearance of the scolex is that of a well-defined four-cornered knob, rectangular *en face*. In the mature worm its width varies from 0·75 to 1·18 mm. and its length from 0·43 to 0·52 mm. Dorso-ventrally it measures from 0·43 to 0·55 mm. Riehm describes the scolex as being 0·75 mm. or more across and states that the breadth is four times the height. The suckers

are large and powerful, varying from 0·23 to 0·29 mm. in diameter, and give the scolex its four-cornered appearance.

Their openings are circular and open directly forward or slightly to the side. They have a faint pigmentation—black.

The sucker wall is very muscular, consisting of a ground tissue of parenchyma bounded by a wall of circular muscle. Through the parenchyma run well-developed strands of muscle fibres. The sucker walls are connected with the wall of the scolex by bundles of muscle fibres, and the bases of the four suckers are connected diagonally by very strongly developed bundles of muscle fibres which cross in the middle line of the scolex.

(*e*) STROBILA. The strobila of the species is very variable. The segments are always broader than long. They are thick, giving the strobila a fleshy appearance and they overlap very markedly. The end segments usually tend to become longer, and sometimes narrower. They are thicker than the more anterior ones, due to their egg content. The genital papillae and cirri have been referred to. They become indistinct in the segments with ripe uteri.

The strobila increases very rapidly in width immediately behind the scolex, there being no neck. Riehm refers to a short flat neck, and describes the worm as up to 80 cms. in length by 15 mm. or more in width, the gravid segments being 3 to 3·5 mm. thick. The specimens taken have been from 30 to 40, even to 70 cms. long consisting of up to 300 segments. In the more typical specimens taken the strobilae vary from 11 to 13 mm. in width. The mature segments vary in length from 0·3 to 0·8 mm. and may be up to 2 mm. in thickness. The gravid segments of such individuals may reach 3 mm. in length by 2–3 mm. in thickness.

The range of variation in the strobila is great. Individuals have been observed in which the mature segments measure up to 2 mm. long. In such a case the segments are usually narrower than is typical, being 6–9 mm. in width, and the segments are not so thick, and overlapping is not so marked. The longest individuals recorded have been of this type. Irregular individuals in which some portions of the strobila consist of very short, wide, and thick segments, and other portions of longer, narrower, and thinner segments have been recorded with fair frequency. The individuals taken from one and the same rabbit are always similar with regard to these external characters of the strobila.

(*f*) MUSCULATURE. The muscular system of the species is very strongly developed. There are two dorsal, and two ventral plates of longitudinal muscle fibres running in large bundles, which are continuous from segment to segment. Anastomosing fibres occur. Near the lateral margins the corresponding dorsal and ventral plates approach and meet except where the base of the cirrus pouch extends into the medullary portion of the segment. At this region the bundles are small. The longitudinal muscle system appears first as a single continuous layer around the bases of the suckers in the scolex. Differentiation into outer and inner layers occurs in the earlier segments.

The circular muscle system consists of a dorsal and a ventral plate lying immediately within the inner plates of longitudinal muscle. These plates are not continuous from segment to segment and the fibres do not run in bundles. A third system of dorso-ventral muscles occurs. It consists of numerous strands running dorso-ventrally in the parenchyma. They are thickly clustered between the segments.

(*g*) Excretory System. In the mature segment the excretory system consists of a dorsal canal and three ventral canals on each side of the segment, the ventral canals of either side being united in each segment by a posterior transverse canal. The wall of the dorsal canal consists of a thick cuticular layer on the inside with an equally thick layer of circular muscle on the outside (Fig. 3). Riehm describes it as being like that of *Dipylidium leuckarti* (= *C. ctenoides*). *C. variabilis* has a similar dorsal canal (Lyman 1902). The diameter of the lumen of the dorsal canal varies from 0·025 to 0·075 mm. with the state of contraction or expansion of the muscular part of the wall. When the muscular part is contracted the cuticular part becomes wrinkled up and has the appearance in transverse section of sending processes into the lumen of the canal. The dorsal canal is surrounded by a mass of small parenchymatous cells with distinct nuclei, distinct from the ordinary parenchyma. The walls of the ventral canals are thin, having no muscular layers, and there are no distinctly differentiated layers of parenchymatous cells around the ventral canals.

Anteriorly in each segment the excretory canals are dorsal in position, the dorsal canal running close to the dorsal muscle plates, one large ventral canal running laterally, and two smaller ventral canals medianly, to it. All the canals run sharply ventrally and somewhat laterally to pass under the lateral genitalia—the prostatic tissue, and vagina.

After passing under the genitalia they all run sharply dorsally, and somewhat medianly, to enter the next segment dorsally. The diameter of the lumen of the large ventro-lateral canal as it passes under the prostatic tissue may be 0·26 mm. The median ventral canal sometimes runs between the receptaculum seminis and the ventral ovarian pouches. Posteriorly in each segment the latero-ventral canal is connected with the other ventral canals by a commissure which passes under the dorsal canal, and the ventral canals on either side are connected by a transverse canal which runs posteriorly to the genitalia in an irregular, branched course. The transverse canal runs in a plane half-way between the dorsal and ventral muscle bands. Secondary longitudinal canals occur. The ventral canals of one side may have connecting and anastomosing branches. The latero-ventral canal was in some segments observed to send a branch to end blindly above the prostatic tissue.

In the younger segments the ventral canal system consists of one canal on either side. In the scolex the two dorsal and two ventral canals run between the suckers. Just anterior to the muscle strands which connect the bases of the suckers the two dorsal canals are connected by a transverse commissure.

In a plane a little anterior to this commissure the ventral canals are similarly connected, and a little more anteriorly the dorsal canal of each side joins the corresponding ventral canal. The two canals so formed fuse to form a single canal which ends blindly in an anterior plane in the scolex.

(*h*) NERVOUS SYSTEM. Riehm describes two three-cornered ganglia, connected by one straight and one horse-shoe shaped commissure in the scolex, and two lateral nerve cords in the strobila. In the present investigation a satisfactory method for the staining of the nervous system has not been found.

(*i*) GENITALIA. There are two sets of reproductive organs in each segment. They appear in anlage very early in the strobila. Both cirrus and vagina open through the very prominent genital papillae situated near the posterior corners of the segments. The papillae become indistinct in the gravid segments.

(i) *Male Genitalia.* The cirrus pouch is very large, its distal portion lying centrally in, and occupying most of the genital papilla. Its base extends into the medullary portion of the segment between the lateral extremities of the muscle plates. It has the form of a cylinder distally, narrowing to a cone medianly, the length of the cone being a little over half that of the cylinder. It has a length of about 0·75 mm. and the cylindrical portion is about 0·26 mm. in diameter. The cirrus pouch consists of the following tissue layers from within outwards:

(1) lumen and cirrus wall; (2) spongy parenchyma through which run longitudinal muscle strands; (3) circular muscle; and (4) longitudinal muscle.

The two muscle layers form the cirrus pouch wall, the circular muscle layer being better developed than that of longitudinal muscle. The wall of the cylinder region of the pouch is well developed medianly, but thins off distally. The wall of the cone region furthest from the base of the pouch is particularly thick, averaging 0·09 mm. in thickness and being principally circular muscle. The wall of the basal region is quite thin and so makes possible the expansion of the cirrus to form a vesicula seminalis when full of sperms.

Around the cirrus pouch is a very well-defined layer of large parenchymatous cells very distinctly marked off from the much smaller cells of the surrounding parenchyma, and separated from it by muscle fibres (Fig. 2).

Strands of muscle fibres run from the base of the cirrus pouch, through the prostatic tissue, medianly and dorsally, to join the dorsal plate of transverse muscle just anterior to the receptaculum seminis.

The cirrus runs a straight course down the centre of the cirrus pouch to pass through its base into the medullary portion of the segment. Distally, the protruded portion of the cirrus may be as much as 0·32 mm. in length. It is covered with numerous, closely set, and sharply pointed cuticular spines about 0·008 mm. long. It is these spines which give the cirri their pigmented appearance. They are not referred to by Riehm. The lumen of the cirrus varies with its content. When not full of sperms it is 0·025 mm. in diameter. When full its diameter may reach 0·06 mm. and its basal portion may be expanded to form a bulb 0·12 mm. in diameter.

The vas deferens leaves the base of the cirrus pouch to run in a median, and somewhat oblique course anteriorly to a point just anterior to the receptaculum seminis. In this portion of its course the vas deferens is surrounded by a mass of prostatic cells, three to four deep, bounded by a thin wall. The course of the vas deferens is convoluted, consisting of loops in a dorso-ventral direction only. This makes the prostatic tissue to appear as one continuous mass, extending from the base of the cirrus pouch to just anterior to the receptaculum seminis, and lying dorsally. Only in section can the arrangement of the prostatic cells around the duct of the vas deferens be seen (Fig. 3). The prostatic tissue extends dorsally to the muscle plates and the loops of the vas deferens are such as to give it a large dorso-ventral diameter, the greatest observed being 0·43 mm. The excretory canals have to dip sharply ventrally to pass under the prostatic tissue. The prostatic cells are regular and well defined and have large faintly-staining nuclei. The diameter of the lumen of the vas deferens in the prostatic tissue varies with its contents from 0·04 to 0·08 mm.

Leaving the prostatic tissue the vas deferens runs, just anterior to the receptaculum seminis and dorsal to the ovary, in a median direction to the testes. Over the lateral portion of the ovary the diameter of its lumen is 0·025 mm. but it becomes smaller as it passes medianly.

The testes are numerous, being scattered in the dorsal field of the proglottid, extending anteriorly to as far as, or a little farther than, the most anterior ovarian pouches, and posteriorly to near the limit of the segment. They extend laterally over the median ovarian pouches, but never reach farther than over the inner portion of the yolk-gland. They are more thickly clustered dorso-ventrally than in mid-field, being 5 to 6 deep just median of the ovary. Testes have been observed in between the ovarian pouches, in some cases far down between the narrower neck-like portions. They are round or oval bodies having a diameter of about 0·129 mm. (Riehm, 0·115 mm.) in the mature segments. In the younger immature segments they are much smaller and are closely packed with deeply-staining nuclei. The nuclei in the mature testes are much larger, and fewer, and cavities occur in which sperms may be observed. No traces of testes remain in the gravid segments.

(ii) *Female Genitalia.* Riehm refers only to the vagina and uterus in any detail, describing the female organs generally as being very like those of *C. pectinata.*

The female organs lie immediately to the inner side of the excretory canals and nearly fill up the lateral field of the segment in the antero-posterior and dorso-ventral directions. The underlying ovary may have a transverse diameter at its greatest of about 1·4 mm. The female organs begin to atrophy with the passage of eggs to the uterus. In the gravid segments traces of the vagina alone remain.

The vaginal pore is posterior to the cirrus and the vagina runs a course ventral and posterior to the cirrus in the genital papilla. It runs at first through, and then just inside the thin muscular wall of the parenchymatous layer which

surrounds the cirrus pouch, being surrounded by a well-defined mass of small irregular cells with distinct nuclei. Distally the wall is strengthened by fine strands of longitudinal muscle fibres. Nearer the base of the cirrus pouch the wall appears thinner. The diameter of the lumen at the distal end of the genital papilla is small, being 0·015 mm. Medianly it widens to about 0·04 mm. Leaving the base of the cirrus pouch the vagina runs in an oblique direction, anteriorly and dorsally, to enter the receptaculum seminis. It runs for some distance along the posterior wall of the prostatic tissue, sometimes in a slight depression in the latter. It is surrounded by a mass of small well-defined cells with distinct nuclei. The diameter of lumen of the vagina in this part of its course is 0·025 mm. The entry of the vagina to the receptaculum seminis is marked by a constriction of its lumen and a thickening of its walls (referred to by Riehm as a valve), and by a marked and constant depression in the wall of the receptaculum seminis. A small dilation of the vagina just lateral to its constriction before entering the receptaculum seminis is frequent but not constant.

The abnormal condition of the vagina passing dorsal to the prostatic tissue and cirrus pouch has been observed with frequency in the material sectioned. It has been observed on only one, and on both sides of a segment.

The receptaculum seminis is a large thin-walled sac, roughly oval in shape, lying dorsally above the latero-ventral pouches of the ovary, its long axis running medianly and posteriorly towards the yolk gland. Its dimensions vary considerably, its length varying from 0·2 mm. to nearly 0·4 mm. and its width from 0·15 to 0·2 mm. It reaches dorsally to near the muscle plates. It is constantly filled with sperms in the mature segments. Closely set strands of dorso-ventral muscle fibres occur anteriorly and posteriorly to the receptaculum seminis. At its medio-ventral extremity the receptaculum seminis gives rise to its duct, which runs medianly and slightly ventrally and posteriorly to a point anterior to, and half-way across, the transverse diameter of the yolk gland. At this point the duct turns in hair-pin fashion dorsally, *i.e.* in a vertical plane. The second arm is very short and receives the oviduct from the basal portion of the ovary. The diameter of the lumen of the receptaculum seminis duct is very variable, being large as it leaves the receptaculum seminis but narrowing medianly to 0·025 mm. or less.

The ovary consists of numerous pouches extending laterally, anteriorly, medianly, posteriorly and dorsally from a common ventral and somewhat posterior reservoir into which they empty by their narrower neck-like portions. Ventrally it extends to the muscle plates underlying all the other female glands, extending anteriorly and posteriorly to near the limits of the segment. It lies just to the inner side of the excretory canals, and extends dorsally to near the muscle plates. Transversely its diameter may be as great as 1·4 mm. The lateral extremity of the uterus runs in between the ovarian pouches anteriorly to receive the uterine duct. Posteriorly the ovarian pouches embrace the vitelline gland. The receptaculum seminis lies dorsal to the latero-ventral pouches of the ovary.

The longer of the pouches are from 0·65 to 0·75 mm. long. The distal club-shaped portions have a diameter of about 0·1 mm. The ovarian pouches are closely packed with large darkly-staining nuclei.

In the material sectioned it was observed that in several segments pouches of the ovary had pierced the ventral muscle plates and extended into the cortical portion of the segment.

The yolk gland is a compact bean-shaped organ with the concavity facing anteriorly. It lies within the ovarian pouches posteriorly, having a posterior limit equal to that of the ovary. It is bounded medianly and laterally by the medio-dorsal and latero-dorsal ovarian pouches respectively. Its transverse diameter is about 0·5 mm. At its greatest diameter dorso-ventrally it reaches very near to the ventral muscle plates and near to the dorsal plate. The yolk gland is tightly packed with very deeply-staining nuclei, smaller than those of the ovary, giving it a coarsely granular appearance. Its wall has shallow, irregular infoldings.

The shell gland lies dorsally between the receptaculum seminis and the medio-dorsal ovarian pouches, directly above the receptaculum seminis duct, its more posterior portion being dorsal to the yolk gland. In some segments it was observed to extend further laterally than the yolk gland. It consists of irregular cells with well-defined nuclei.

The oviduct arises from the common ventral reservoir of the ovary just anterior to the yolk gland. The point of origin is a little median of a point half-way across the transverse diameter of the yolk gland. The duct runs dorsally and slightly laterally for a distance of about 0·2 mm. to receive the receptaculum seminis duct. Its lumen has a diameter of 0·012 mm. The wall is very thick and surrounded by a single layer of small parenchymatous cells with large distinctly staining nuclei.

The duct formed by the combination of those of the ovary and the receptaculum seminis enters the shell gland ventrally. It is surrounded by a mass of small cells, one to two deep, with large distinct nuclei. In the shell gland it forms a dilation 0·012 mm. in diameter which is surrounded by a mass of small cells, much smaller than the ordinary cells of the shell gland, with distinct nuclei.

The yolk gland duct arises from a dorsal and anterior point in the yolk gland, to the inner side of the centre of the shell gland. It runs a straight course, laterally and dorsally, for a distance of 0·09 mm. to enter the base of the dilation of the combined ducts of the ovary and receptaculum seminis in the shell gland. The wall of the duct is surrounded by small cells with distinct nuclei. Its lumen has a diameter of about 0·013 mm. as it leaves the yolk gland, but becomes much smaller nearer the shell gland.

From the dilation in the shell gland arises the uterine duct, which runs dorsally through the shell gland and then runs a convoluted course anteriorly above the shell gland. The diameter of its lumen is 0·01 mm. Reaching the anterior limit of the shell gland it turns ventrally and runs medio-ventrally

to enter the lateral extremity of the uterus. The uterine duct is surrounded by a mass of small parenchymatous cells with distinct nuclei.

The uterus is a simple reticulum running across the segment anteriorly about half-way between the dorsal and ventral muscle plates. Its extremities extend laterally a little over half-way across the transverse diameters of the ovaries to receive the uterine ducts. Clustered around its wall are small parenchymatous cells with distinct nuclei. Riehm described the uterus "not as a simple tube widened here and there and running transversely across the segment, but it is broken up into two or three such tubes which unite here and there and so cut up the parenchyma into islands. This structure is seen however only in segments without eggs. Through the pressure of developing ova these tubes widen so that the islands of parenchyma are suppressed, and the uterus appears as a single tube." The uterus also increases its capacity by the growth of proximal and distal pouches. The reproductive organs atrophy and the gravid segment becomes a swollen mass of eggs with strands of parenchyma here and there. The excretory system persists in the parenchyma on either side. Traces of the cirrus pouch and vagina remain.

(*j*) OVA. The eggs are globular, but they may lose their original shape by pressure or shrinkage in the uterus. They average 0·054 mm. in diameter.

The embryo is surrounded by a pyriform apparatus, the bulb of which measures 0·025 mm. in diameter. The bulb is produced into a pair of horns, thick at the base but becoming thinner, long and filamentous distally. The hexacanth hooks of the embryo are easily distinguished. They measure 0·008 mm. in length.

3. COMPARISONS WITH THE DESCRIPTION OF RIEHM (1881).

The differences between the descriptions of Riehm and that of the present writer are considerable. Although the writer does not consider himself justified in claiming to have described a new species, particularly without an examination of the original material of Rudolphi and that of Riehm, he considers it desirable to call attention to these differences and to place them on record. They are given below. A copy of Riehm's drawing of a mature segment is given for comparison (Fig. 4).

(*a*) TESTES. Riehm: "Scattered throughout the dorsal field."

The illustration (Fig. 4) shows them extending laterally over the genitalia as far as the excretory canals, and anteriorly a considerable distance in front of the ovary.

Writer: In the dorsal field, 5–6 deep just median of the ovaries, extending in over the ovaries, but never further than the most median portion of the yolk gland. Extending anteriorly as far as, or a little farther than, the most anterior plane of the ovaries (Fig. 1).

(*b*) VAS DEFERENS AND PROSTATIC TISSUE. Riehm: Vas deferens has "as simple a course as possible" from the median field to the base of the cirrus pouch. Prostatic tissue in a contracted segment appears as "a compact organ

more or less cup-shaped, still we can discern in an extended segment that the apparently compact gland consists of a single tube folded in several layers and clothed with glandular epithelium. Comparable to that of *Taenia rhopalocephala*." The illustration shows the vas deferens running from the cirrus pouch into the median field in front of the ovary, and the prostatic tissue clustered as several cup-shaped masses around the base of the cirrus pouch.

Writer: The vas deferens runs from the base of the cirrus pouch to a point just anterior to the receptaculum seminis in a series of dorso-ventral loops, this portion of the duct being surrounded by prostatic tissue (Figs. 1 and 3). The prostatic tissue appears at first sight as one mass. Leaving the prostatic tissue the vas deferens runs just anterior of the receptaculum seminis and dorsal of the ovary to the median field (Fig. 1).

(*c*) Retractor Muscles of Cirrus Pouch. Riehm: Pass from base of cirrus pouch to median of the excretory canals anterior to the vas deferens (Fig. 4).

Writer: Run from base of cirrus pouch through the prostatic tissue, to join the dorsal plate of transverse muscles just anterior to the receptaculum seminis.

(*d*) Cirrus Pouch Wall. Riehm: Provided with three layers of muscles, two circular and one longitudinal.

Writer: Cirrus pouch wall consists of two muscle layers, circular muscle on the inside, and longitudinal on the outside.

(*e*) Female Genitalia. Riehm: "Essentially the same as in *C. pectinata*." The drawing shows the ovarian pouches spread out apparently in one horizontal plane, and not distended distally, so as to be club-shaped. No ovarian pouches underlying, or extending over, the yolk gland. No ventral reservoir of ovary. Ovarian duct arising considerably anteriorly of the yolk gland. Yolk gland duct arising from a point lateral to the middle point of the yolk gland. Vagina shown as running outside the parenchymatous layer which surrounds the cirrus pouch.

Writer: Ovary underlies all the other female glands; consists of numerous club-shaped pouches extending laterally, anteriorly, medianly, posteriorly, and dorsally, from a common ventral, and somewhat posterior, reservoir. The female genitalia nearly fill up lateral field of segment in antero-posterior and dorso-ventral directions. Oviduct arises from reservoir of ovary just anterior to the yolk gland at a point a little median of a point half-way across the yolk gland. The yolk gland duct arises from a point median of a point half-way across the yolk gland. The vagina runs in the parenchymatous layer surrounding the cirrus pouch and then along the posterior edge of the prostatic tissue.

(*f*) Uterus. Riehm: The drawing shows the uterus extending across the segment beyond the excretory canals. (No reference to the extent of the uterus is made in the text of the description.)

Writer: The extremities of the uterus extend laterally in between the ovarian pouches, a little over half-way across the transverse diameters of the ovaries, to receive the uterine ducts.

Riehm records an abnormality, which he observed: "now and again," of a third set of female reproductive organs in one segment occurring right or left of the median line, in which a receptaculum seminis never occurred, and in which the yolk gland was sometimes wanting.

4. On Attempts to Elucidate the Life-Histories of *Cittotaenia denticulata* and *Cittotaenia pectinata*.

No attempt has been made to discover the life-histories of the *Cittotaenia* spp. occurring in rabbits, and very little seems to be known about their occurrence. The examinations of large numbers of rabbits recorded in this paper were made in the hope that the occurrence and distribution of *Cittotaenia denticulata* (Rudolphi 1804) and *C. pectinata* (Goeze 1782) would indicate factors influencing their life cycles. In addition certain experimental work has been done on the assumption of the necessity for the intervention of an intermediate host.

Mature individuals of *C. denticulata* occur either singly or, more usually, in pairs. On no occasion have more than two mature individuals been taken from one rabbit. Young forms have been recorded most frequently in small numbers only from individual rabbits—often only one, sometimes four or five. One one occasion however, in August, 37 young *C. denticulata* of various ages were taken from one rabbit. As many as 40–50 mature individuals of *C. pectinata* together with a greater number of young forms have been taken from individual rabbits, but smaller numbers are usual.

In none of the rabbits examined were *C. denticulata* and *C. pectinata* recorded from the same individual. Even where infection has been recent and heavy, and large numbers of young forms occur, there has been no evidence of multiple infection. No observation parallel to this appears in the literature on rabbit cestodes. Jenkins (1924) observes that with *Moneizia* infection in lambs, "the usual condition is that the tapeworms found in one lamb are of one species. The rule however is not invariable as *M. expansa* and *M. translucida* have been found in one individual, as have *M. expansa* and *M. alba*." The possibility of this phenomenon of mutual exclusion being one of locality has been explored, and it has been found that, in most of the localities examined, both species of cestodes do occur. On one occasion 20 rabbits were ferreted from a hedge-bank some 200 yards long intersected by rabbit burrows. Nine of the rabbits were infected with *C. denticulata* and four with *C. pectinata*. The remaining seven were free from cestodes. In one locality however, in the Aeron Valley, near Aberaeron, 155 rabbits were examined, of which 125 were infected with *C. pectinata*. *C. denticulata* did not occur.

It may be that a rabbit already infected with one of the spp. *C. denticulata* or *C. pectinata* is refractory to infection by the other.

(*a*) Infection and Soil Conditions. Douthitt (1915) states in his conclusions that, "the cestodes of the sub-family Anoplocephalinae are in some ways dependent upon rich soils for their existence and they thrive best in wet lowlands." In the present investigations rabbits from a variety of soils ranging from good damp, or wet, clay land, to poor dry land, have been examined and infection with *Cittotaenia* has been observed in all. Jenkins (1924) found a similar range of infection with *Moneizia* spp. in lambs. The results of the examinations of the rabbits from the various areas are given in Table I.

Table I.

Area	Type of soil	Number of rabbits examined	Number infected with *C. pectinata*	Number infected with *C. denticulata*	Total % infected	% infected with *C. pectinata*	% infected with *C. denticulata*
Llanllyr, Aeron Valley	Fertile, wet, alluvial	155	125	—	80	80	—
Crosswood, Aberystwyth	Fertile, fairly dry, and light land	69	48	6	78	69	9
Bridgend, Vale of Glamorgan	Fertile, heavy clay land	88	41	8	56	47	9
Tanybwlch Cliffs, Aberystwyth	Poor, rather dry land	91	24	39	68	25	43

Tapeworms are reported to be prevalent in the rabbits of Ynyslas sand hills. Only three have been examined. Each was infected with *C. denticulata.*

The most one is justified in concluding from these examinations is that infection with *Cittotaenia* spp. takes place under a variety of soil conditions, and that there are indications that the more fertile soils favour infection with *C. pectinata,* and the less fertile with *C. denticulata.*

Neither *C. denticulata* nor *C. pectinata* have been reported from domestic rabbits. Nine have been examined. They were free from cestodes. Riehm (1881) records *C. ctenoides* in the domestic rabbit in Saxony.

(*b*) Occurrence and Period of Infection. Since it has been impossible to examine rabbits from any one area in large numbers, at every season of the year, no complete statement as to the occurrence and the period of maximum infection can be made. The majority of the rabbits examined have of necessity been those killed during the "season"—the autumn and winter. The data collected show that rabbits are heavily infected, and infection takes place all the year round. Infection appears to be heavier in late winter than in autumn (cf. Riehm (1881), who states that *C. pectinata* occurs in European hares only in the autumn and first half of the winter).

Early in January 66 rabbits were examined from the Vale of Glamorgan. Six of them harboured *C. pectinata,* 3 in large numbers. Later in the same month 28 of 70 rabbits from the Aeron Valley were found to be infected with young *C. pectinata*—very large numbers of young cestodes occurring in 8 of them. During March, 69 rabbits were examined from Crosswood, from 10 of which young *C. pectinata* were taken—one young cestode from each rabbit (in

addition to mature individuals). Several of the rabbits examined in August 1924 harboured 50 to 100 young *C. pectinata* in addition to mature individuals. In a small number of the rabbits examined from September to December, young *C. pectinata* were found in small numbers.

In a small percentage of the rabbits examined during the autumn, winter and early spring small numbers—usually one, sometimes four or five—young *C. denticulata* have been found, pointing to infection throughout that period. In August 1924, 37 young *C. denticulata* were taken from one rabbit.

Twelve young rabbits, not fully grown, have been examined. No adult cestodes were found.

(*c*) WORK DONE ON THE ASSUMPTION OF AN INTERMEDIATE HOST. A certain amount of work has been done on the assumption that the life-histories of *Cittotaenia* spp. resemble those of the great majority of cestodes in requiring the intervention of an intermediate host. If this is so, the intermediate host is probably some small invertebrate which the rabbit ingests incidentally to grazing. Since infection has been seen to take place all the year round it must occur even when the invertebrate fauna of herbage is most limited, *i.e.* during the winter months. And since heavy infection of individual rabbits may take place, even during the winter months, the intermediate host must (assuming the larval cestode to be of the simple type) be common.

(*d*) EXAMINATIONS OF STOMACH CONTENTS OF RABBITS. At different times extending over the period of investigation the complete stomach contents of 8 rabbits have been examined under the binocular microscope. The object of the investigation was to see with what frequency, if at all, invertebrates were ingested incidentally to grazing, what size invertebrates might be so ingested, and if any indication were given as to the nature of the intermediate host. The results of the examinations are given below:

Aug. 3rd	The crushed abdomen of an insect	
Sept. 29th	13 mites	0·5 to 0·8 mm. in length
Oct. 11th	1 wingless aphid	
Oct. 20th	No invertebrates	
Oct. 25th	2 mites	0·7 mm. in length
Dec. 12th	2 mites	0·6 mm. in length
Feb. 2nd	No invertebrates	
March 13th	1 adult carabid beetle	1·3 mm. long and a portion of a larger insect

When it is borne in mind that a rabbit eats sufficient to fill its stomach several times in one day, and that the examinations of stomach contents have been done chiefly during the winter months when the invertebrate fauna of herbage is very limited, it will be seen that invertebrates are ingested with appreciable frequency. Only mites and the smaller insects have been found intact, but the crushed portions of insects found point to the possibility of the ingestion of larger forms. It seems probable that during the summer months feeding rabbits ingest considerable numbers of invertebrates.

(*e*) FEEDING EXPERIMENTS. In carrying out feeding experiments invertebrate forms which occur all the year round, and whose structure and habitat

make it appear possible for them to ingest *Cittotaenia* eggs under natural conditions, have been dealt with. The faeces of those forms which were found to ingest eggs have been examined. In this way it appears possible that the existence of four groups of invertebrates will be found:

(1) Those which do not ingest *Cittotaenia* eggs; (2) those which ingest the eggs and pass them unchanged with the faeces; (3) those which ingest the eggs and whose digestive juices cause disintegration changes in the eggs; (4) those which ingest the eggs and in which further development of the eggs takes place, *i.e.* the intermediate hosts of *C. denticulata* and *C. pectinata*.

In all the experiments conducted eggs of both *C. denticulata* and *C. pectinata* have been used.

In the rabbit faeces examined only two dung beetles have been found—*Aphodius punctato-sulcatus* and *Oxytelus sculpturatus*. In addition to these, other beetles living on the dung of herbivorous animals have been experimented with. Except in the case of *Oxytelus sculpturatus* the *Cittotaenia* eggs were mixed with the faeces of sheep for the experimental feeding.

Aphodius punctato-sulcatus. Two batches were taken, one fed on faeces with which had been mixed large numbers of *Cittotaenia* eggs, the other placed in a dish with gravid *Cittotaenia* segments. Three specimens from each batch were dissected under the binocular microscope, and the contents of their alimentary canals were removed and examined. *Cittotaenia* eggs of both species were found in all. An examination of the faeces of the remaining specimens showed that the eggs were passed unchanged.

Aphodius fimetarius. Two batches were taken as before and treated similarly. Two specimens from each group were dissected. The faeces of the remaining specimens were examined. The results were the same as for *A. punctato-sulcatus*.

Oleochara lanuginosa. A number of specimens were fed on dung containing large numbers of *Cittotaenia* eggs. Four were dissected and the contents of their alimentary canals examined. Eggs of both the *Cittotaenia* species were found in all. An examination of the faeces of the remaining specimens showed that the eggs were passed through unchanged.

Gercyon melanocephalus. Two batches of specimens were taken, one fed on dung containing numerous *Cittotaenia* eggs, the other placed with gravid segments. Three specimens from each batch were dissected. The eggs of both species were found in all. No traces of eggs could be found in the faeces it was possible to obtain for examination.

Sphaeridium quadrimaculatum. Two specimens fed on dung containing *Cittotaenia* eggs were dissected. Eggs were found in their alimentary canals. Sufficient specimens to allow of an examination of the faeces after experimental feeding were not obtained.

Oxytelus sculpturatus. Six specimens were fed on rabbit faeces with which large numbers of *Cittotaenia* eggs had been mixed. On dissection and examination of their alimentary canals no eggs were found.

Three small Staphylinid species were found to be common in herbage during the winter months:

Stenus lactifrons. S. speculator. Tachyporus chrysomelinus.

The possibility of their occasionally feeding on the gravid *Cittotaenia* segments passed in rabbit faeces was considered. A number of specimens of each species were placed in a dish containing gravid *Cittotaenia* segments. They were never observed to feed on the segments. The dissection and examination of several specimens of each species showed no trace of ingested eggs.

Free-living mites are common in herbage during the winter. A number of specimens of *Pergamasus crassipes*, var. *longicornis*, one of the commonest and largest species, were enclosed in a jar with fresh grass thoroughly brushed over with *Cittotaenia* eggs. After 5 days, 9 of the specimens were killed and embedded in wax and examined by means of serial sections. No eggs were found.

Spilopsyllus cuniculi. The rabbit flea is very common during the warmer months of the year, less common during the winter. The possibility of its acting as an intermediate host has been considered. Experimental feeding is not possible. Eighteen fleas were embedded in wax and examined by means of serial sections. No trace of eggs in the alimentary canal, or of developmental stages in the tissues, was found.

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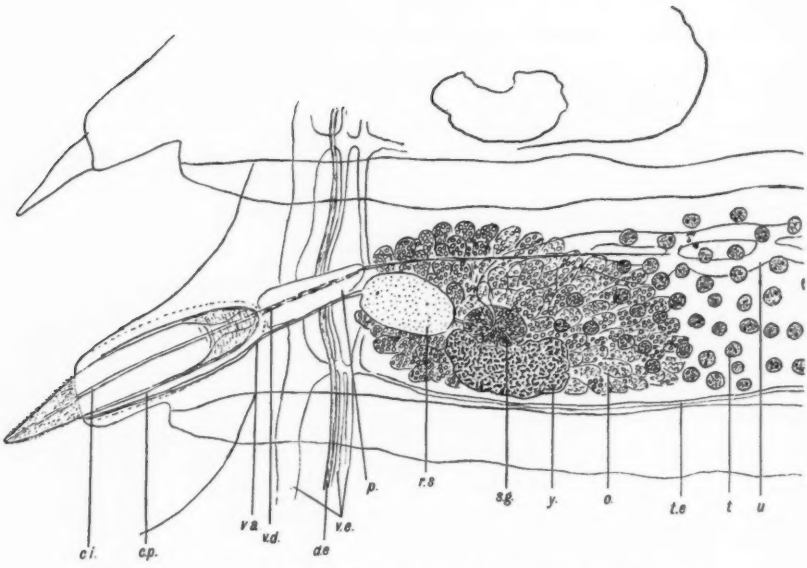

Fig. 1. Reconstruction of the right half of a mature proglottid. ×42.

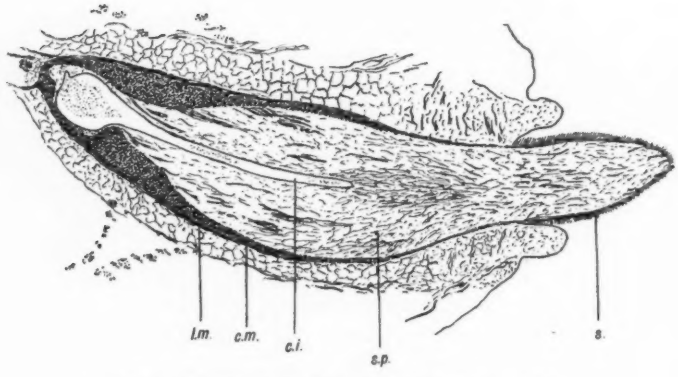

Fig. 2. Transverse section of a cirrus pouch. ×120.

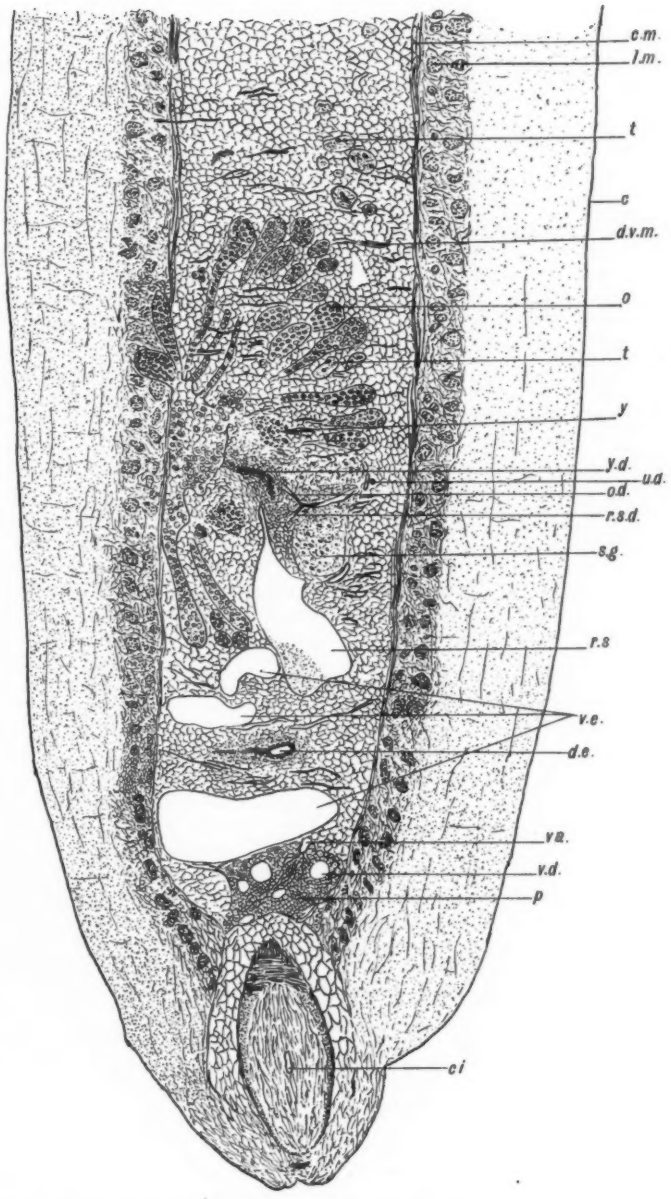

Fig. 3. *Cittotaenia denticulata* (Rudolphi 1804). Transverse section of a mature proglottid. × 60.

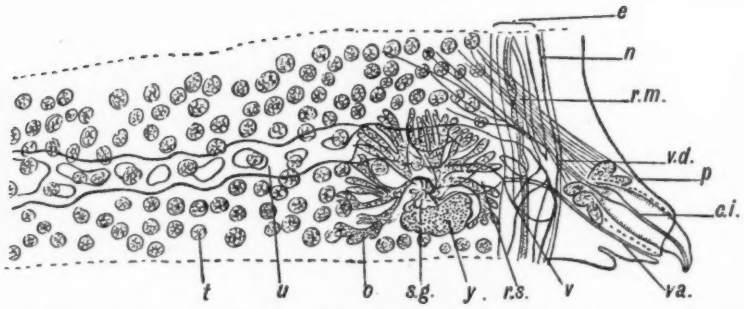

Fig. 4. *Cittotaenia denticulata* (Rudolphi 1804). Copy of Riehm's drawing of a mature segment.

LETTERING.

c. cuticle; *c.i.* cirrus; *c.m.* circular muscle; *c.p.* cirrus pouch; *d.e.* dorsal excretory canal; *d.v.m.* dorso-ventral muscles; *e.* excretory canals; *l.m.* longitudinal muscles; *n.* nerve cord; *o.* ovary; *o.d.* oviduct; *p.* prostatic tissue; *r.m.* retractor muscles of cirrus pouch; *r.s.* receptaculum seminis; *r.s.d.* receptaculum seminis duct and oviduct; *s.* spines; *s.g.* shell gland; *s.p.* spongy parenchyma and muscle strands; *t.* testis; *t.e.* transverse excretory canals; *u.* uterus; *v.* "valve"; *va.* vagina; *v.d.* vas deferens; *v.e.* ventral excretory canals; *y.* yolk gland; *y.d.* yolk duct.

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